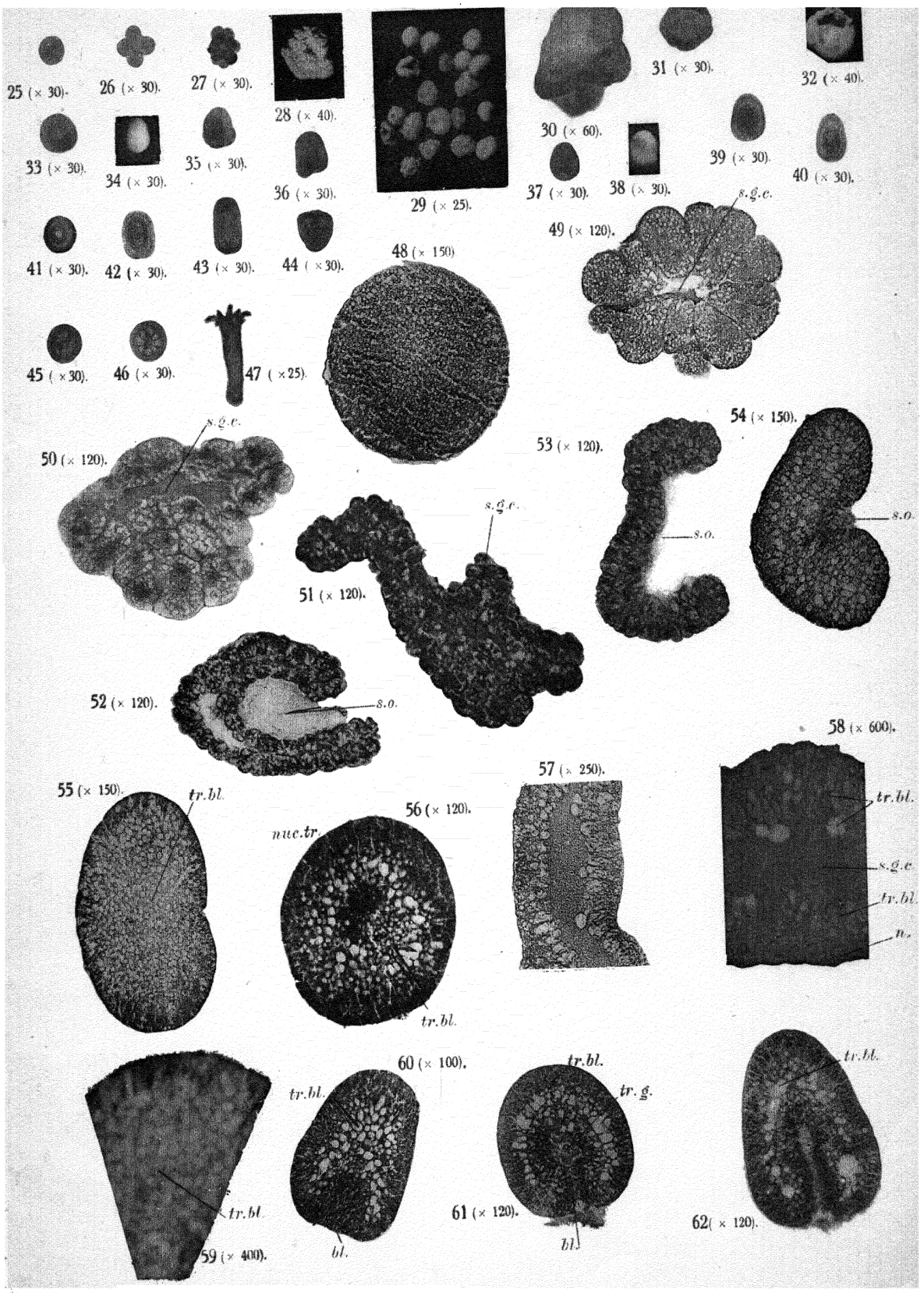
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# PHILOSOPHICAL

# TRANSACTIONS

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# ADVERTISEMENT.

THE Committee appointed by the *Royal Society* to direct the publication of the *Philosophical Transactions* take this opportunity to acquaint the public that it fully appears, as well from the Council-books and Journals of the Society as from repeated declarations which have been made in several former *Transactions*, that the printing of them was always, from time to time, the single act of the respective Secretaries till the Forty-seventh Volume; the Society, as a Body, never interesting themselves any further in their publication than by occasionally recommending the revival of them to some of their Secretaries, when, from the particular circumstances of their affairs, the *Transactions* had happened for any length of time to be intermitted. And this seems principally to have been done with a view to satisfy the public that their usual meetings were then continued, for the improvement of knowledge and benefit of mankind: the great ends of their first institution by the Royal Charters, and which they have ever since steadily pursued.

But the Society being of late years greatly enlarged, and their communications more numerous, it was thought advisable that a Committee of their members should be appointed to reconsider the papers read before them, and select out of them such as they should judge most proper for publication in the future *Transactions*; which was accordingly done upon the 26th of March, 1752. And the grounds of their choice are, and will continue to be, the importance and singularity of the subjects, or the advantageous manner of treating them: without pretending to answer for the certainty of the facts, or propriety of the reasonings contained in the several papers so published, which must still rest on the credit or judgment of their respective authors.

It is likewise necessary on this occasion to remark, that it is an established rule of the Society, to which they will always adhere, never to give their opinion, as a Body,

upon any subject, either of Nature or Art, that comes before them. And therefore the thanks, which are frequently proposed from the Chair, to be given to the authors of such papers as are read at their accustomed meetings, or to the persons through whose hands they received them, are to be considered in no other light than as a matter of civility, in return for the respect shown to the Society by those communications. The like also is to be said with regard to the several projects, inventions, and curiosities of various kinds, which are often exhibited to the Society; the authors whereof, or those who exhibit them, frequently take the liberty to report, and even to certify in the public newspapers, that they have met with the highest applause and approbation. And therefore it is hoped that no regard will hereafter be paid to such reports and public notices; which in some instances have been too lightly credited, to the dishonour of the Society.

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# VIII. —*The Transition from Rostro-carinate Flint Implements to the Tongue-shaped Implements of River-terrace Gravels.*

*By* J. Reid Moir.

*Communicated by* Sir Ray Lankester, *K.C.B., F.R.S.*

(Received October 19, 1917,—Read December 13, 1917.)

[Plates 51–57.]

The object of this communication is to describe and figure accurately seven flint implements of peculiar form, which have been found in certain ancient valley gravels in different parts of this country, and to put forward an explanation of the meaning and significance of these specimens, which appears to the author to be reasonable and in accord with probability.

## *A Detailed Description of the Colour, Condition, etc., of the Seven Specimens, together with an Account of their Provenance.*

### *List of Specimens.*

1. The Savernake transitional specimen No. 1.
2. The Savernake transitional specimen No. 2.
3. The Dawley transitional specimen.
4. The Mildenhall transitional specimen.
5. The Clapton transitional specimen.
6. The Ipswich transitional specimen.
7. The Axminster transitional specimen.

1. The Savernake Transitional No. 1 (Plate 51, figs. 1, 2, 3, 4). Found in a gravel pit at Knowle Farm, Savernake. The specimen, which is yellowish brown in colour, has been fashioned by the removal of large flakes, and a number of cracks are observable in its mass. The flint, which shows but few signs of having been abraded by rolling by water, exhibits, nevertheless, some evidence of contusion on its edges, and this is especially marked on the upper dorsal ridge. A small number of incipient cones of percussion (due to the impact of other stones) are visible upon its flake-scars, and with a lens a few small striæ are observable upon its surfaces, which exhibit, moreover, a moderate amount of glaze.* The natural cortex of the flint has been left at the posterior region of the implement, which is also marked by the presence of a considerable cavity, which must have been present in the original nodule of flint from which the specimen was fashioned. A small patch of cortex is

* The term "glaze" is used to denote the naturally-produced bright, smooth surface exhibited by many ancient flint implements. The cause or causes giving rise to such surfaces, are at present unknown.

present also upon the dorsal surface of the implement. This specimen, together with that next to be described, was acquired by the Reverend H. G. O. KENDALL from the workmen at the Knowle Farm pit, and very kindly presented to the author. The gravel at Knowle Farm occurs at a height of approximately 450 feet O.D., and 40 to 50 feet above the base of the neighbouring dry valley.

2. THE SAVERNAKE TRANSITIONAL NO. 2 (Plate 52, figs. 1–4).—This specimen, which exhibits signs of considerable abrasion due to rolling by water, is light chestnut-brown in colour, and the flake-scars which have been formed by the removal of large flakes do not exhibit a marked glaze. A considerable number of incipient cones of percussion, and small criss-cross striæ, are developed upon the flaked surfaces of the implement. In places where the striations are most numerous, the flint has assumed a bluish-white coloration. The specimen exhibits patches of cortex upon its right and left lateral, dorsal, and ventral surfaces. Several cracks are observable in its mass, and a rectangular fracture, induced in all probability by one of these lines of weakness, is to be seen at the posterior region of the implement.

3. THE DAWLEY TRANSITIONAL (Plate 53, figs. 1–4).—Found in 1893, in "Odell's Pit," Dawley, situated near West Drayton, in the Thames Valley. The specimen was recovered by the late Mr. ALLEN BROWN at a depth from the surface of 21 feet. The gravel in which the implement occurred rested beneath a deposit of brickearth, and has been identified as forming part of the 100-foot terrace of the Thames.* The specimen, which is ochreous-brown in colour, has been fashioned by the removal of large flakes. It exhibits a considerable amount of abrasion, and the dorsal ridge has suffered extensive contusion, caused possibly by use. A few incipient cones of percussion and some well-marked striæ are observable upon some of its flake-scars, which show also a peculiar pitting of the surface. The implement does not exhibit a marked glaze, and a patch of cortex is to be seen towards the posterior end of the left lateral surface. One or two cracks are present in its mass. This specimen, together with the two next to be described, have passed into the author's possession, owing to the kindness of the late Dr. W. ALLEN STURGE.

4. THE MILDENHALL TRANSITIONAL (Plate 54, figs. 1–4).—Found in the famous implementiferous gravel bed at Warren Hill, near Mildenhall, Suffolk. This specimen was originally in the possession of the late Mr. WORTHINGTON G. SMITH, who, it is supposed, acquired it from one of the workmen in the Warren Hill pit. The implement exhibits over much of its surface the peculiar mottled yellow and black coloration present on a large number of the Warren Hill flints. The other portions of its surface are a lightish brown in colour, while some later edge-flaking is patinated a light blue. This specimen has been fashioned by the removal of large flakes, and has suffered some amount of abrasion due to rolling by water. A considerable number of incipient cones of percussion and a few small striæ are developed upon the flaked surfaces, which exhibit a moderate amount of glaze.

* 'Memoirs Geol. Survey,' "The Geology of the London District," pp. 89–90.

The posterior region of the implement is composed of unflaked cortex, and one or two cracks are observable in the mass of the flint.

5. The Clapton Transitional (Plate 55, figs. 1-4).—Found in a bed of implementiferous gravel at Clapton, in the Thames or Lea Valleys. The specimen was originally in the possession of the late Mr. Greenhill, whose collection of flint implements was purchased by the late Dr. W. Allen Sturge. The Clapton gravel bed forms, apparently, part of the 50-foot terrace of the Thames Valley.* The implement, which shows considerable abrasion due to rolling by water, exhibits a dark red-brown coloration over parts of its surface and a lighter brown in others. The surfaces of the specimen, which are well glazed, bear a few incipient cones of percussion and some well-marked striæ. Under a lens the large flake-scars show a peculiar pitted appearance, and several cracks are developed in the mass of the flint. A small patch of cortex is observable at the posterior region of the implement.

6. The Ipswich Transitional (Plate 56, figs. 1-4).—Found by a workman, employed by the author, in a bed of implementiferous gravel situated in a shallow valley upon the plateau to the East of Ipswich. The gravel occurs at a height of about 120 feet O.D. The specimen, which has been fashioned by the removal of large flakes, exhibits various colours, ranging from a putty shade to ochreous brown, upon its surfaces. It is extensively abraded and rolled and a few incipient cones of percussion are observable upon the flake-scars. The implement is considerably striated, and a few cracks are developed in its mass. It is only very slightly glazed and has a patch of cortex at the posterior region.

7. The Axminster Transitional (Plate 57, figs. 1-4).—Found in the well-known gravel pit at Broom near Axminster, Somersetshire. The bed in which the implement occurred rests at a height of about 150 feet O.D. (Evans, "Ancient Stone Implements of Great Britain," second edition, p. 639). The specimen was acquired from a workman in the pit by Mr. A. S. Barnes who kindly presented it to the author. The implement which is considerably abraded is formed of chert and is greyish-yellow in colour. The flake scars are of medium size and exhibit only a slight glaze. A patch of "cortex" is observable at the posterior region of the specimen.

The foregoing details, and the excellent drawings of the implements accompanying this paper, executed by Mr. Leonard Squirrell of Ipswich, will, it is hoped, enable the reader to form an accurate mental picture of the seven specimens which form the subject matter of this communication.

It is clear from the evidence afforded by their provenance that these seven implements are of a considerable antiquity, and this view is further supported by evidence of a different character. In each case, with the exception of the Axminster specimen (Plate 57, figs. 1-4), the bold and somewhat rough flaking responsible for the form of the implements is of the kind associated with a comparatively early stage in

* 'Memoirs Geol. Survey,' "The Geology of the London District," p. 91.

man's efforts to shape flints to his needs. Further the colour and condition of the flints are of an antique order, and finally each of the specimens has been found in association with other implements exhibiting the same method of flaking, and of a similar colour and condition which, by their form, are referable to the earliest palæolithic, river-drift series. The chert specimen from Broom pit though, apparently not so ancient as the others, is, nevertheless, by its form assignable to an early stage in the history of river-drift man. It seems clear then that these seven implements may, with some amount of certainty, be regarded as of early palæolithic age.

*The Peculiar Form of the Implements.*

If reference is made to the illustrations of the seven specimens under consideration (Plate 51, figs. 1–4), (Plate 52, figs. 1–4), (Plate 53, figs. 1–4), (Plate 54, figs. 1–4), (Plate 55, figs. 1–4), (Plate 56, figs. 1–4), (Plate 57, figs. 1–4), it will at once be noticed that all of them exhibit in profile a marked beak-like appearance. This likeness to the beak of an accipitrine bird is caused by the downward curvature of the dorsal ridge and its junction with the much straighter ventral surface. A further reference to the illustrations will show that the specimens found at Knowle Farm Pit, Savernake (Plate 51, figs. 1–4, and Plate 52, figs. 1–4), at Warren Hill (Plate 54, figs. 1–4) and in the Thames Valley (Plate 53, figs. 1–4 and Plate 55, figs. 1–4) are all furnished with a more or less flat ventral surface, and that each of them, especially towards the anterior region, are approximately triangular in section. The implements, on the other hand, found at Ipswich (Plate 56, figs. 1–4), and at Axminster (Plate 57, figs. 1–4), do not exhibit the flat ventral surface. In fact this surface has been replaced by a ventral ridge and the section of the implements has become roughly rhomboidal.

In 1911 Sir Ray Lankester described before the Royal Society the series of flint implements found beneath the Pliocene Red Crag of Suffolk, to which he gave the name of "rostro-carinate." Of these particular specimens he states*: "In the Pre-Crag implements the anterior narrow edge, though tending to the vertical, is strongly curved and gives the implement the form of the beak of an accipitrine bird. The form of this region of the implement may also be compared to that of the prow of a boat (the boat being turned keel upwards). We distinguish (keeping the prow or beak to the front) an upper or dorsal plane, a lower or ventral plane, a right lateral and a left lateral surface, a posterior surface or stern, usually very irregular, heavy and roughly shaped as though for holding in the hand, and an anterior surface, narrowed to the form of a keel and ending in a beak (hence we call the implement 'rostro-carinate'), as a consequence of the oblique direction and convergence of the lateral surfaces, which approach one another so as to leave only a narrow keel-like ridge between them. We usually see this keel or 'carina' reaching forward from the broad, middle and posterior portions of the upper surface of the implement, as a very

* 'Phil. Trans.,' B, vol. 202, pp. 294–295.

distinct and leading feature in its sculpture." Sir RAY LANKESTER illustrates the foregoing remarks by means of three diagrams showing the ideal form aimed at by the makers of the Pre-Crag rostro carinate flint implements, and the author has copied these diagrams which are shown in fig. 1.

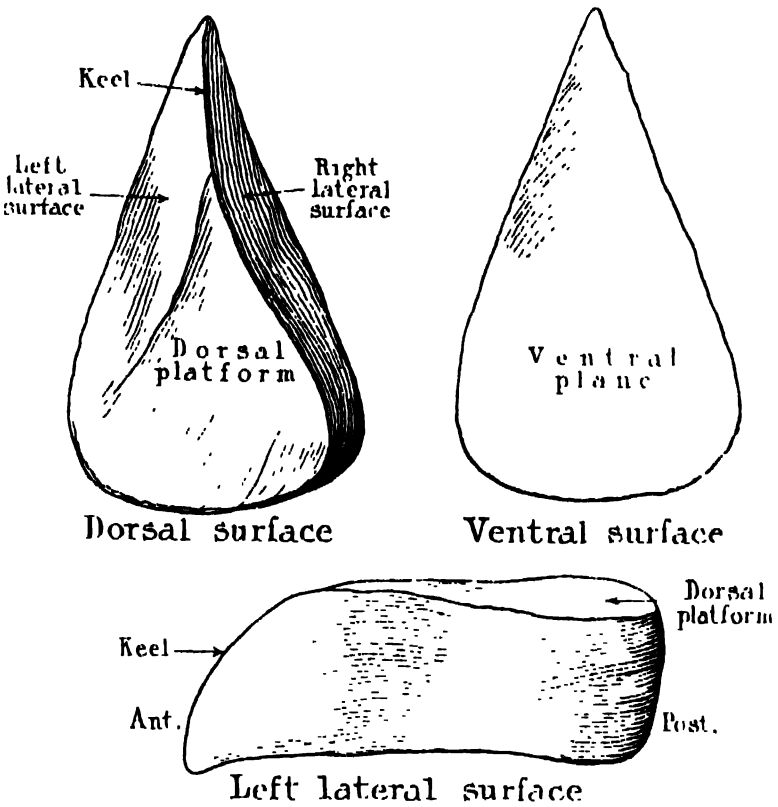



FIG. 1.

If the reader will now apply Sir RAY LANKESTER'S description of a rostro-carinate flint implement to the specimens illustrated (Plate 51, figs. 1–4; Plate 52, figs. 1–4; Plate 53, figs. 1–4; Plate 54, figs. 1–4; Plate 55, figs. 1–4), it will be realised that these implements, though of palæolithic river-drift age, are of the rostro-carinate type, but they are better made and more highly evolved than those found below the Red Crag and in other pre-river-valley deposits. The two other specimens illustrated (Plate 56, figs. 1–4) and (Plate 57, figs. 1–4), though exhibiting the beak-like profile, cannot be regarded as true rostro-carinates owing to the fact that they do not possess the more or less flat ventral plane. Four views of each of the seven implements are given and their various characteristics are indicated clearly (Ant. = Anterior and Post. = Posterior). A sectional drawing of each specimen is also provided.

### *An Explanation of the Peculiar Form of the Seven Specimens.*

In giving an explanation of the peculiar form of the seven specimens under examination, it is necessary, first of all, to deal with the question of flint flaking. To

be able to flake flints with a hammer stone successfully, it is needful to either select a stone with a natural flat surface upon which flake removing blows may be delivered with precision, or to produce such a surface by means of a heavy blow with the hammer-stone. This flat surface is necessary, because the hammer-stone cannot generally "get home" on a rounded surface, but glances off ineffectually. The production of a flat surface, or "striking-platform" as it is called, is of fundamental importance in flint flaking, and it is not surprising, therefore, to find that through the whole period when flint implements were in use its paramount necessity was recognised. The Pre-Crag rostro-carinate implements afford an excellent example of such recognition. As has been already pointed out, the section of a rostro-carinate implement is more or less triangular.

The base of the triangle represents the broad ventral surface, and this surface, in the author's opinion, is simply a flat striking-platform upon which blows were delivered in the formation of the sharp keel or carina, which is represented by the apex of the triangle. But, in addition to the ventral surface, the rostro carinate implements very often exhibit a well-marked dorsal platform, and this, in the author's opinion, may be regarded as the remains of another striking-platform. In many experiments in the flaking of flint which have been carried out, he has found it to be necessary in producing a symmetrical rostro-carinate to deliver blows upon the dorsal surface as well as upon the ventral. Hence it is necessary, in setting out to fashion such an implement from a nodule of flint, to provide two striking-platforms, a dorsal and a ventral. The author would like to here state that the discovery of the necessity for the production of two such striking-platforms in the formation of a symmetrical rostro-carinate implement was first made by Sir RAY LANKESTER. In his account of a remarkable implement of this type, found by Mr. W. G. CLARKE, Sir RAY LANKESTER states that in his opinion it is probable that the ancient flint-worker who fashioned this particular specimen "having selected a good sound flint nodule of first-rate quality . . . proceeded to break it by two great cleaving blows into a *tabular* form. . . ."*

The author acting upon this suggestion carried out experiments with several large rounded nodules of sound flint, and found that it was possible to produce, by flaking, a piece or "chunk" of tabular flint from such nodules, as had been adumbrated by Sir RAY LANKESTER. In fig. 2 a diagram is given showing how such production is accomplished. The continuous line represents the outline of the rounded nodule of flint. A heavy blow is struck at the point A, and the line of fracture, shown by the dotted line (the direction of the force responsible for the cleavage is indicated by an arrow), continues to the point B. The portion of the flint nodule above the line A-B is thus removed, and a flat surface produced. Another heavy blow is then delivered at the point C, and the line of fracture continues to the point D. The portion of the flint

* "Description of the Test Specimen of the Rostro-carinate Industry found beneath the Norwich Crag," Roy. Anthr. Inst., 'Occasional Papers,' No. 4, p. 8.

nodule below the line C–D being thus removed, a second flat surface is produced. Having accomplished this, a by no means easy task, it is possible to proceed to the fashioning of the rostro-carinate implement.

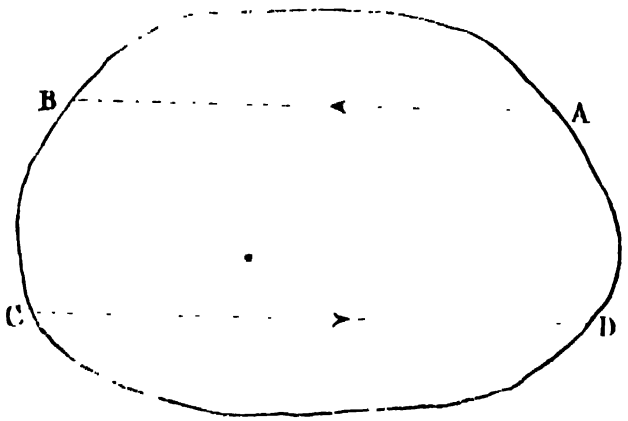



Fig. 2.—Production of Tabular Flint from Rounded Nodule.

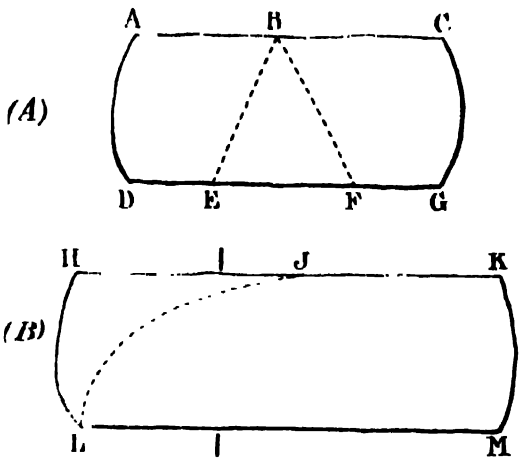



Fig. 3.

If reference is now made to fig. 3A, which shows the piece of tabular flint and a rostro-carinate in section, it will be realised how such an implement is produced. Blows are delivered upon the flat lower surface between D–E and F–G, and upon the flat upper surface between A–B and B C. These blows result in the formation of the triangular section of the rostro-carinate as indicated by the dotted lines E B F, and remove the portions of the tabular piece of flint contained within the continuous and dotted lines A D E B and B F G C. In fig. 3B the piece of tabular flint and the rostro-carinate implement are shown in profile, and the curving keel of the implement is indicated by the dotted line L J. It will be noticed that the original flat lower surface L–M remains as the ventral plane of the rostro-carinate, while a portion only of the original flat upper surface H K is retained and forms the dorsal platform of the implement. This portion lies between J and K.

In the Norwich test specimen of the rostro-carinate industry described by Sir Ray Lankester the method outlined above appears to have been carried out in almost every detail. A diagrammatic drawing of the left lateral surface of this implement is given in fig. 4, and a comparison of this illustration with fig. 3B will show how nearly the profiles of the two rostro-carinates resemble each other.

The author is of opinion that the sharp keel or carina of the rostro-carinate implement was the object at which the ancient workmen were aiming. They required a good cutting edge for various purposes, and the curving keel of the rostro-carinate gave them what they wanted. In a paper published recently,* the author has shown that with the wish to provide a longer cutting edge the sharp keel was gradually carried further and further back towards the posterior region of the implement, and

* 'Journ. Roy. Anthrop. Inst.,' vol. 16, pp. 197–220 (1916).

that this extension of the keel was accompanied, inevitably, by the reduction in size of the dorsal platform. He also drew attention to the fact that from the Pre-Crag

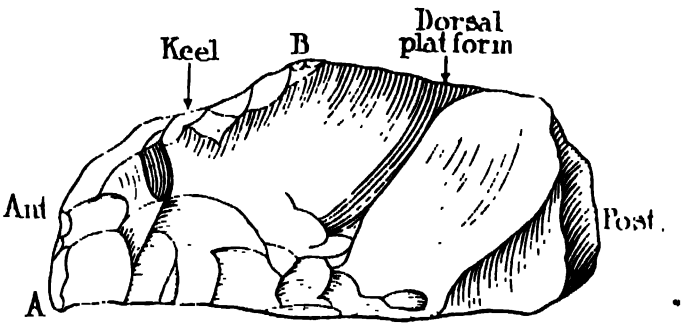



Fig. 4. -Left Lateral Face of Norwich Test Specimen. (Somewhat reduced in size.)

period onwards the width of the ventral plane suffers a marked reduction. The Post Crag rostro-carinates, in fact, show an ever-increasing tendency to be compressed from side to side. In the Middle Glacial Gravel of Suffolk, a deposit later in age than the Red Crag, a series of rostro carinates has been found which shows clearly the characteristics above described. A diagrammatic drawing of one of these rostro-carinate implements from the Middle Glacial Gravel is given in fig. 5, and it will be seen

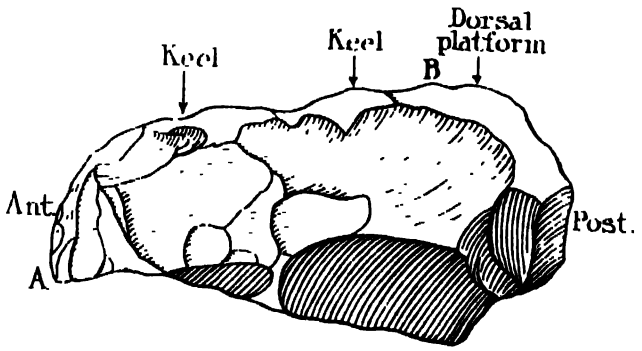



Fig. 5. Left Lateral Face of Rostro-Carinate from Middle Glacial Gravel, Ipswich. (Somewhat reduced in size.)

that in the Norwich test specimen (fig. 4) the point B, which represents the furthest extension of the keel towards the posterior region (the keel commences at the point A), is situated about in the middle of the dorsal surface of the implement, whereas in the Middle Glacial specimen the backward extension of the keel is greater, and in consequence the distance between A and B is more extended. This extension of the keel towards the posterior region of the implement was carried on until in many cases the dorsal platform disappeared entirely, and the implement from Clapton (Plate 55, figs. 1–4), already described, affords an excellent example of this type. It is the author's opinion that in these implements the flat ventral surface rested against the palm of the hand when being used, while the sharp keel was used as a cutting and scraping edge. Implements of the type found at Clapton (Plate 55,

figs. 1–4) have been collected for some years and classed as palæolithic "side-choppers," but whether this designation is correct or not, it seems clear that they are simply "compressed" rostro-carinates, in which the keel has been extended to the posterior region, and which, in consequence, do not exhibit any dorsal platform.

We may suppose that having at length produced an implement with a cutting edge extending the whole length of one side of the flint he had fashioned, it occurred to the ancient flint worker that it would be an advantage to make another cutting edge opposite to the first one, and extending the whole length of the other side of the flint. We know that this was accomplished because the pointed and ovate palæolithic implements with two cutting-edges can be brought forward in evidence. The question is, how was it accomplished?

The author has experimented extensively in the flaking of flint, and he has found that the only way in which it is possible to provide a rostro-carinate with a cutting edge *directly opposite* to the keel or carina is to flake away each side of the ventral plane, and so to produce a sharp edge. In fig. 6 the triangle formed by continuous lines shows the section of a rostro-carinate implement, the apex A represents the keel while the base B–D represents the flat ventral plane. To produce a cutting edge at C, opposite to A, it is necessary to deliver blows principally upon the ventral surface between B–C and between C–D. In this process the portions of the rostro-carinate limited by continuous and dotted lines, and indicated by the numerals 1 and 2, are removed, and the resulting implement assumes in section a roughly rhomboidal form. Fig. 7 shows the edge-view of a palæolithic implement (continuous lines) as it would appear when the necessary portions of the ventral plane of the rostro carinate had been flaked away. The outline of the ventral plane is indicated by dotted lines. If any representative series of palæolithic river-drift implements is examined it will be seen that the majority exhibit a more or less rhomboidal section, and it is the author's opinion that the earliest river-drift implements were evolved from the rostro-carinate type in the manner indicated. The author has himself produced, by flaking, an implement of river-drift type by first of all fashioning the flint into a rostro-carinate, and then proceeding to transform the flat ventral plane into a cutting edge. But he does not wish to claim that the ancient flint workers in making a pointed "palæolithic" implement always began by flaking the flint into a rostro-carinate form. He wishes only to suggest that the knowledge of the necessity for the provision of two flat striking-platforms in the making of a pointed palæolithic implement was acquired by the makers of the rostro-carinate specimens, and that this knowledge was handed on and preserved by the peoples who lived after them. But it is necessary to emphasise the fact that the method of preparing a nodule of flint for the production of a rostro-carinate is precisely the same as that needed for the production of a pointed palæolithic, river-drift implement. The flint is first of all shaped to a tabular form as in the case of the rostro-carinate (figs. 3A and 3B), and in fig. 8A the tabular piece of flint and the palæolithic implement are

shown in section. In the formation of the rhomboidal outline blows are delivered upon the upper flat surface of the piece of tabular flint between A–B and B–C, and

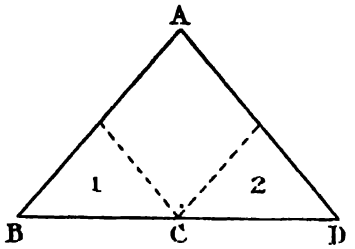
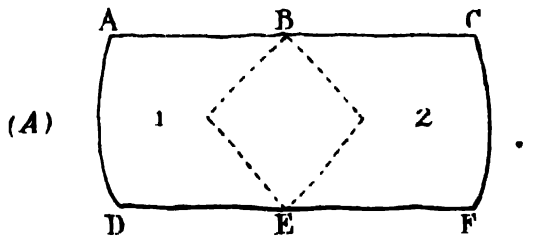



Fig. 6.



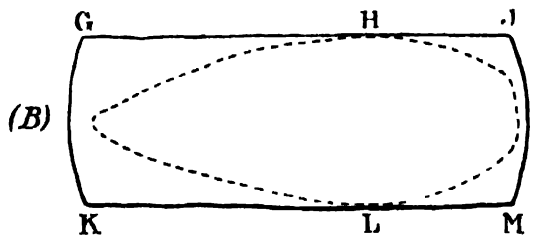




Fig. 8.

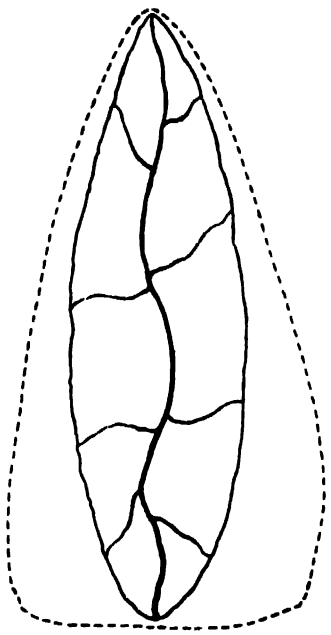


Fig. 7.

upon the lower flat surface between D–E and E–F. In this process the two portions of the tabular flint limited by continuous and dotted lines, and indicated by the numerals 1 and 2, are removed. In fig. 8B the piece of tabular flint and the palæolithic implement are shown in profile, and it will be noticed that the only portion of the original flat surface G J is retained at H, and the only portion of the surface K M is retained at L. At these two points, H and L, a small flat area of the original surfaces will be seen intersecting the edges of the palæolithic implement, and in many specimens from the river-drift these vestiges of the large original striking-platforms are observable towards the posterior region of the implements. Sometimes, as would be expected, only one such platform is to be seen, and many palæolithic implements of the latest river-drift type do not show them at all. Their retention or elimination depended solely upon the amount of trouble taken by the ancient flint worker in finishing his implement. These restricted areas of the large striking surfaces have been known to archæologists as lateral platforms but their significance has not been fully recognised. When the palæolithic implement is regarded, as is usually the case with the point uppermost, such platforms are correctly

described as being lateral. But if these implements are posed in the rostro-carinate manner (as in fig. 8B), then the small platforms become dorsal or ventral as the case may be, and their true significance can be recognised. The ovate palæolithic implements, which are simply specimens having a rounded cutting edge instead of a point, very often exhibit, as would be expected, remains of the large original striking-platforms.

Many pointed palæolithic implements, especially those referable to the earliest river-drift deposits, very frequently show in profile a quite marked beak-like appearance. The author has found, in fashioning a flint into the form of a pointed palæolithic implement, by the method already described, that quite unconsciously the rostro-carinate profile is preserved, and he supposes that the efforts of the ancient flint workers had occasionally a similar result. But if, as is supposed, the palæolithic implements were evolved from the rostro-carinate type, then it is only natural that the outline of the parent form should at times make itself manifest.

It thus seems reasonable to conclude that the early palæolithic river-drift implements are directly evolved from the more ancient rostro-carinate specimens (the author wishes it to be clearly understood that he does not at present associate the later Mousterian, Aurignacian, Solutrean, and Magdalenian cultures with this evolution), and we may proceed to examine the seven implements which it is the main purpose of this paper to describe, and to ascertain whether they support this theory of evolution.

Before, however, proceeding to such a description it may be well to again emphasise the fact that these seven specimens have all been found in deposits of gravel well known as yielding numerous specimens of the earliest examples of the handiwork of river-drift man. These seven specimens also exhibit the same colour and other conditions of surface exhibited by the normal implements from the gravel beds, and it appears necessary to conclude therefore that they are of the same age as the aforesaid normal palæolithic implements.

1. *The Savernake Transitional Specimen No.* 1 (Plate 51, figs. 1–4).

This implement, as will be seen from the four views illustrated, possesses all the characteristics of a rostro-carinate, as set forth earlier in this paper. The views of the right and left lateral surfaces (figs. 1 and 2) show the well-known beak-like profile (in the drawing of the right lateral surface the artist has tilted the implement over somewhat so that a portion of the ventral plane—darker shading—is visible). Fig. 3 shows the more or less flat ventral plane, while fig. 4, which illustrates the dorsal surface of the specimen, shows the keel sweeping back from the anterior region to the dorsal platform, which in this case is somewhat marred by a cavity evidently present in the original nodule of flint from which the implement was made. The implement is, moreover, more or less triangular in section. We may regard this specimen then as a true rostro-carinate showing flaking of a more advanced order than the Pre-Crag

and other early examples of this type, and its presence in the valley gravel at Knowle Farm affords evidence that occasionally the palæolithic flint flakers made typical rostro-carinate implements.

2. *The Savernake Transitional Specimen No.* 2 (Plate 52, figs. 1–4).

This specimen, also from Knowle Farm, Savernake, exhibits some remarkable characteristics. The drawings of the right and left lateral surfaces (figs. 1 and 2) show the well-marked beak-like profile. The remains of the narrow flat ventral plane are shown in the drawing of the ventral surface of the implement, and occur immediately under the point of the beak. The remainder of the ventral plane has been flaked away (fig. 3) and it seems evident that the intention was to provide a cutting edge in place of this ventral plane. The drawing of the dorsal surface shows also that the keel extends but a little way back from the point of the beak, while the dorsal platform is of considerable extent as indicated by the two widespread dotted lines (fig. 4). The author has studied this specimen very carefully and considers that it represents an unfinished implement. The intention of the ancient flint flaker was to produce a pointed palæolithic implement, but for some reason his work was never completed. This specimen demonstrates the correctness of the description given above (p. 337) of the manner in which a palæolithic implement was made, and its beak-like profile shows that, in this method of manufacture, the flint assumed at one stage the rostro-carinate form. The two sectional drawings show clearly the dual character of this implement. That taken through the line B B is more or less triangular and, therefore, of the rostro-carinate order. The section through the line A–A shows the beginnings of a cutting edge at the point C, while the upper, dorsal platform is seen to be almost intact. At the posterior region of the implement too an attempt has evidently been made to produce a cutting edge, and this feature, unknown in any Pre-Crag or other early rostro-carinates hitherto discovered, shows distinct palæolithic affinities. This implement presents then characteristics of the rostro-carinate specimens and the earliest pointed river-drift palæoliths, and it may be regarded as a transitional form between these two types of flaked flints.

3. *The Dawley Transitional Specimen* (Plate 53, figs. 1–4).

This implement found at Dawley in the Thames Valley is an excellent example of the highly-evolved rostro-carinate of the early river-drift palæolithic deposits. Such specimens as these were found years ago and preserved as examples of what are known as "palæolithic side-choppers." It is possible, as has been already pointed out, that this designation is correct because the flat ventral plane would afford a comfortable surface for prehension, while the sharp keel might be used for chopping and cutting purposes. But an examination of the four drawings of the specimen will show that we are dealing with an undoubted rostro-carinate. The right and left lateral surfaces (figs. 1 and 2) exhibit the usual beak-like profile, the narrow ventral

surface (fig. 3) though formed by several flake-scars, is more or less flat, while the dorsal surface (fig. 4) shows the keel extending from the anterior region to the much truncated remains of the dorsal platform situated at the posterior end of the implement. All of which characteristics, though in a highly evolved degree, are typical of the rostro-carinate industry. The sectional drawing is roughly triangular, which is in accord with the above determination. We may regard this specimen as affording evidence that, as at Knowle Farm, Savernake, the early river drift men of the Thames Valley occasionally made rostro-carinate implements, and it should be noted that as in Specimen No. 2 from Knowle Farm (Plate 52, figs. 1–4) a rough cutting edge, in the early palæolithic manner, has been formed at the posterior end of the implement.

4. *The Mildenhall Transitional Specimen* (Plate 54, figs. 1–4).

This implement from Warren Hill, Suffolk, represents, in the author's opinion, a similarly unfinished specimen to that from Knowle Farm, Savernake, already described (p. 340). The right and left lateral surfaces (figs. 1 and 2) are beak-like in profile; the narrow ventral surface (fig. 3) shows towards its anterior limit evidence of the first attempts to produce a cutting edge, while the dorsal platform is of considerable extent as indicated by the widespread dotted lines (fig. 4). The keel, in consequence, does not extend very far back towards the posterior region (fig. 4). The section taken through the line B-B shows the triangular form of the rostro-carinate type, while that through the line A–A shows the dorsal and ventral surfaces to be left almost intact. This specimen, then, appears to afford evidence that, as at Knowle Farm, Savernake, the early river-drift men of N.W. Suffolk fashioned their pointed implements on what may perhaps be termed the rostro-carinate plan.

5. *The Clapton Transitional Specimen* (Plate 55, figs. 1–4).

This specimen found at Clapton may, like the implement from Dawley in the Thames Valley, be classed as a highly evolved rostro-carinate. The right and left lateral surfaces and the comparatively narrow ventral surface (figs. 1–3) are all in accord with this determination. The dorsal surface (fig. 4) exhibits the keel extending continuously from the anterior to the posterior region, accompanied by the inevitable disappearance of the dorsal platform. The sectional drawing is triangular in form.

We have thus arrived at the stage as shown by this specimen, when the keel of the rostro-carinate extends continuously from one end of the dorsal surface to the other, and this marks the culminating point in the production of this type of implement. In the fashioning of an implement having two opposite cutting edges a change is made from the simple triangular section to one roughly rhomboidal. The method by which this change was in all probability accomplished has been already described (p. 337) and a diagram given (fig. 6) in illustration of this description. But it must be remembered that diagrams are ideal, while the ideal in manipulating a

refractory and peculiar material like flint is seldom attained. Though, therefore, in the diagram mentioned (fig. 6) the author has shown the second cutting edge at C to be immediately under the keel at A he does not wish to convey the impression that such accuracy was often attained by the ancient flakers of flint. As a matter of fact the point C may be located almost anywhere along the line B-D, and the truth of this statement will become manifest in the implements now to be described.

6. *The Ipswich Transitional Specimen* (Plate 56, figs. 1–4).

This Ipswich specimen, though a very early palæolithic, river-drift implement, possessing two cutting edges, presents certain characteristics strongly reminiscent of the rostro-carinate form. The right and left lateral surfaces (figs. 1 and 2) show a well-marked beak-like profile, while the massiveness of the posterior region of the implement is such as is usually seen in rostro-carinate specimens. It is when we turn to the ventral and dorsal surfaces, however, that the importance and interest of this Ipswich implement becomes manifest. An examination of the drawing of the ventral surface (fig. 3) shows clearly that the maker of this implement intended to form his cutting edge in a straight line from the anterior to the posterior region. He began his task well and the cutting edge is seen to take a straight course posterior-wards for about an inch and a half from the anterior region. Then for some reason or another, it swerves suddenly to the right, and curves gradually to the posterior extremity of the implement. When the drawing of the dorsal surface is examined it is seen that this asymmetry of the cutting edge presents a very similar form. Again we see the cutting edge taking a straight course posterior-wards for a little distance, and then swerving off to the right. The author can only explain this peculiarity by suggesting that the ancient flint flaker was not quite master of his work, as it would have been quite possible to have made both the dorsal and ventral cutting edges straight. It does not seem possible that the asymmetry of these edges could make the implement more useful or a better cutting instrument, whereas it seems reasonable to suppose that straight cutting edges would have increased its efficiency. If it were feasible to regard the two areas (indicated in the drawings by crosses, figs. 3 and 4) as the remains of the original dorsal and ventral surfaces of the implement, and to say that the anterior portions of these two surfaces were in process of being transformed into cutting edges, while their other portions remained intact, our difficulties would disappear. But it is not feasible to come to such conclusions in regard to these surfaces. The two areas indicated by crosses on the dorsal and ventral surfaces are by no means flat, as is shown in the sectional drawing. Moreover, by the manner of the truncation, and direction of the blows forming the flake-scars which compose these two dorsal and ventral areas, it is clear that they have been struck from pre-existing flat surfaces which in the formation of the two cutting edges have been entirely flaked away. If reference is now made to fig. 9 and to the sectional drawing (Plate 56) it will be seen that this implement is roughly rhomboidal

in section. In fig. 9 an outline of the section (continuous line) is placed in a more or less triangular "frame" (dotted line). If a comparison is made between this

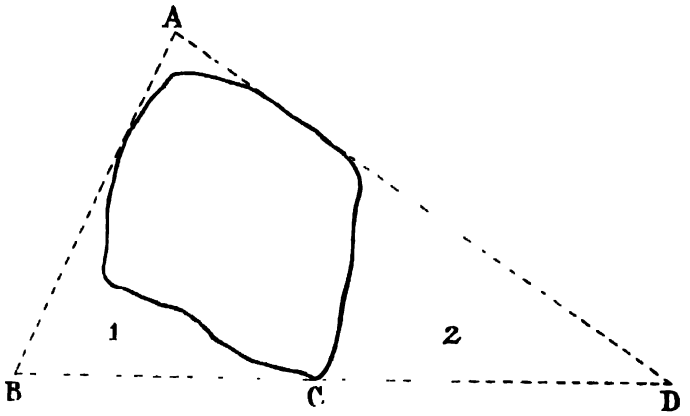



FIG. 9.

diagram (fig. 9) and the ideal diagram shown above (fig. 6), it will be seen that there is not any very fundamental difference observable. In the ideal diagram the point C is immediately under A, while in the other (fig. 9) this is not so. But in both cases the areas indicated by the numerals 1 and 2 have been removed by flaking after the flint had been shaped into the triangular form of the rostro-carinate implement. Altogether this curious, unsymmetrical specimen seems to combine the characteristics of a definite double-edged palæolithic implement, with many rostro-carinate affinities, and the author regards it as an excellent example of a very early clumsy palæolithic implement just emerging, so to speak, from the rostro-carinate stage, and showing in consequence many evidences of its parentage.

### 7. *The Axminster Transitional Specimen* (Plate 57, figs. 1–4).

There is no need to write very much in reference to this symmetrical palæolithic implement from Somerset. The drawings of the right and left lateral surfaces

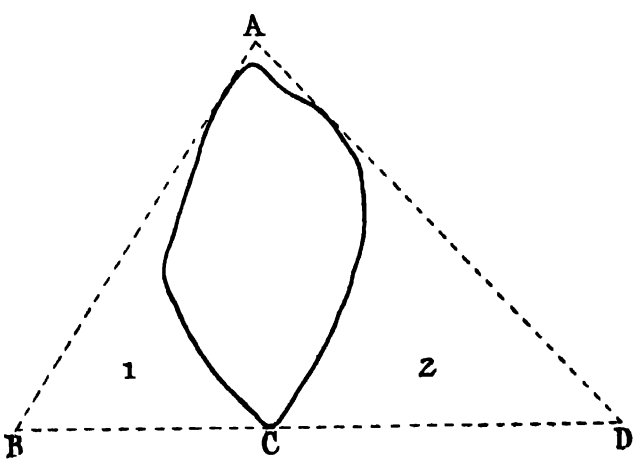



FIG. 10.

(figs. 1 and 2) demonstrate that in profile it has a marked beak-like appearance, while the views of the ventral and dorsal surfaces (figs. 3 and 4) show that the cutting edges take a straight course from the anterior to the posterior region. In section the implement is roughly rhomboidal in form, and in fig. 10 it will be seen that its symmetry is such that the point C is immediately under A as in the ideal diagram above (fig. 6). This specimen is of interest as an example of an early symmetrical palæolithic river-drift implement still retaining the rostro-carinate profile.

*Conclusion.*

The foregoing examination of the seven implements has demonstrated that in early river drift times, rostro-carinate implements of a highly evolved type were in use contemporaneously with the normal pointed, palæolithic specimens.

These river-drift rostro-carinates exhibit more elaborate flaking, and keels more extended towards the posterior region of the implements than is found in earlier examples of this type. The dorsal platform of the later type of rostro-carinates has either been eliminated by the extension of the keel to the extreme limit of the posterior region or has become much reduced in size. It appears also that the rostro-carinate implements from Pre-Crag times onwards underwent a process of compression accompanied by a reduction in width of the ventral plane, and that this reduction culminated in the production of a cutting edge in place of the more or less flat ventral surface. With the production of a second cutting edge, opposite to the primary keel or carina, the earliest river-drift, palæolithic implement made its appearance. The section of the rostro-carinate implement is triangular, the base of the triangle representing the flat ventral surface, and when this surface was transformed into a cutting edge the section of the resulting implement became roughly rhomboidal. The manner in which the change from the triangular to the rhomboidal form was brought about has been described (fig. 6), and two of the specimens illustrated (Plate 52, figs. 1–4, and Plate 54, figs. 1–4) appear to be unfinished and to exhibit, as would be expected, characteristics of the rostro-carinate and early river-drift implements. The specimen found at Ipswich (Plate 56, figs. 1–4), though a very early river-drift implement of pointed type with two cutting edges, was seen to possess some well marked rostro-carinate characters, and it appears to have been made by someone inexpert in the fashioning of such specimens. The apparently dual character of this implement would lead to the conclusion that at this period the earliest river-drift palæolithic specimens were being made, and that the inexpertness of the flint flaker is in consequence not unexpected.

It was seen that the pointed palæolithic implement of the river-drift was made in fundamentally the same way as the rostro-carinate, that is, the original nodule of flint was so fractured as to offer two large and more or less flat striking-platforms, upon which flake-removing blows could be struck with precision (figs. 8A and 8B). These striking-platforms in the rostro-carinate implements form the dorsal and ventral

planes, while in the palæolithic implements they appear as small platforms intersecting the cutting edges, and situated towards the posterior region of the specimens. The early palæolithic implements, in many cases, exhibit a beak-like profile, which, together with the afore-mentioned platforms, afford evidence of their derivation from a rostro-carinate shaped flint.

It will be noticed that the seven implements selected for illustration and description come from widely separated localities, and this fact, apart from any other, would appear to shut out any possibility of these specimens being merely chance products due to some abnormal method of fashioning flint implements practised by some isolated community of early river-drift people. We appear to be dealing with a widespread and, as the author believes, inevitable method of implement making. For, in addition to the seven specimens here described, he has seen and handled many specimens of early river-drift "side-choppers," in reality highly evolved rostro-carinates, in the following public and private collections. In the British Museum (Bloomsbury) there are two from Shrub Hill, Norfolk; one from Aylesford, Kent; three from Swanscombe, Thames Valley; one from Brandon, Suffolk; two from Hill Head, Southampton; and one from Kent's Cavern, Torquay (8-foot level). In the Ipswich Museum there are three from Suffolk (Warren Hill, Lakenheath, Mildenhall); and one from Canterbury. Dr. W. Allen Sturge, of Icklingham Hall, also informed the author that his vast collection contained several examples of this type of implement.

The author has found that the symmetrical river-drift implements with two cutting edges which still retain the rostro-carinate profile are even more numerous than the so-called "side-choppers." The late Sir John Evans in his well-known book "Ancient Stone Implements of Great Britain," second edition, figures five such specimens (Nos. 429, 436, 448, 445D, 458), and the author has seen many others in public and private collections.

Sir Ray Lankester has drawn the attention of the author to the fact that the *shape* of the palæolithic implement bears the same relation to the rostro-carinate as does a flat-fish (plaice) to a dog-fish. The section of a dog-fish and a rostro-carinate is roughly triangular (fig. 11), while the section of a palæolithic implement and a flat-fish bear a great resemblance to each other (fig. 12). Sir Ray Lankester lays

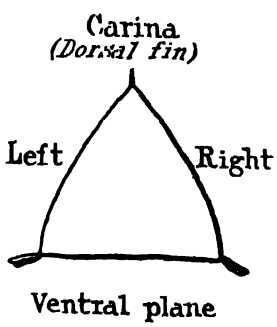



Fig. 11.—Section of Dog-fish and Rostro-Carinate.

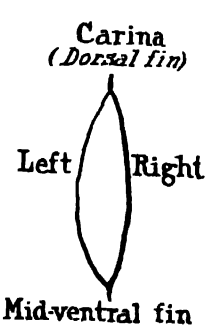



Fig. 12.—Section of Plaice and Palæolith.

stress on the remarkable fact that the *symmetry* of the palæolithic implement is like that of the flat-fish, produced by removing flakes from each side of the rostro-carinate, which takes the place of the "compressing" by which the flat-fish is shaped. We should naturally *expect* that the palæolith would be produced by *depressing* the rostro-carinate, as the flattened skate is produced (fig. 13), but it is

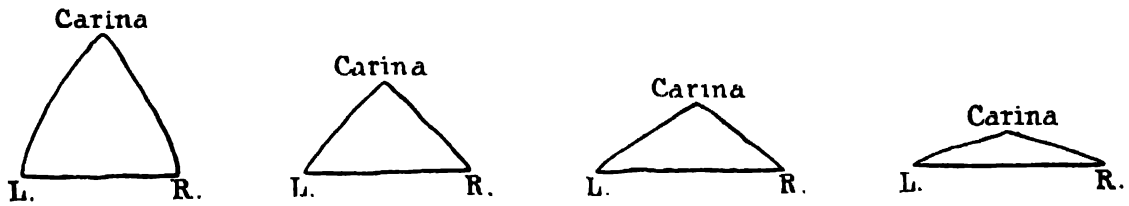



Fig. 13.

not. It is produced as the plaice is produced by converting the right and left *sides* of the original form into new dorsal and ventral surfaces, or, as one may say, remoulding the whole shape, so that the original dorsal carinal ridge becomes one edge of a new dorsal surface, and the rest of the flint is trimmed to a new symmetry accordingly (fig. 14).

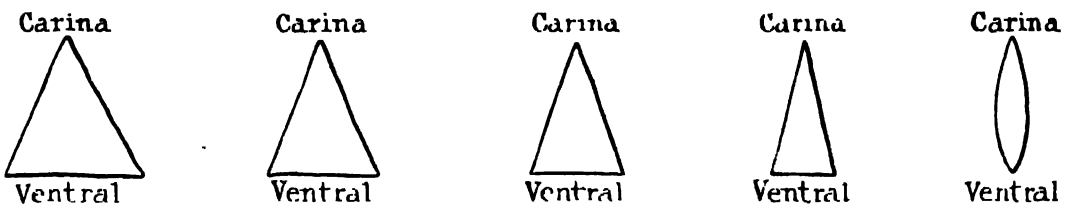



Fig. 14.

Sir Ray Lankester considers that the word "Platessiform" might be applied in future to all the palæoliths derived from rostro-carinates, or they might be called "Latero-carinate," meaning that the carina had taken a lateral position, and with this view the author is in agreement. In this paper no attempt has been made to deal with the geological considerations involved in the relative ages of the most ancient valley gravels, and the Pre-Crag and other deposits from which the earliest rostro carinates have been derived. Such a subject could only be discussed with any profit by expert geologists, familiar with the beds in which the implements have been found. But such geological considerations, though of importance, are distinct and separate questions, and cannot influence in any way the reality of the evolution described in this communication.

[*Note Received October* 16, 1918.—Since the above was written the author's attention has been directed to a series of palæolithic flint implements,* occurring in

* These were first described by Mr. Henry Bury, see 'Proc. Prehis. Soc. E. Anglia,' vol. 2, Part 2, pp. 365–374.

some abundance in the deposits of the Chellian period, which do not exhibit the usual rhomboidal section referred to in this paper. The particular specimens dealt with in this note are triangular in section and thus approximate even more closely to the rostro-carinate form than do those implements which exhibit a rhomboidal section. The nodules of flint from which these specimens with triangular section were made were operated upon in two different ways. (1) By detaching a large flake from one end, and directing flake-removing blows upon the flat surface thus produced in forming the upper, dorsal portion of the implement, and (2) by splitting the nodule into two pieces, in the direction of its greatest length, and manipulating one or both of these pieces in the manner described above. In nearly every case the posterior end of the implements exhibits unflaked cortex which appears to have been left to allow of comfortable prehension, while very frequently the lower ventral surface shows flake-scars caused by blows delivered upon the side of the latero-ventral edges. But it is somewhat difficult to understand why such flakes were removed, as the specimens which exhibit the flat, untrimmed ventral surface appear to be in every way as useful for cutting and thrusting purposes. Fig. 15 illustrates an implement of triangular section from

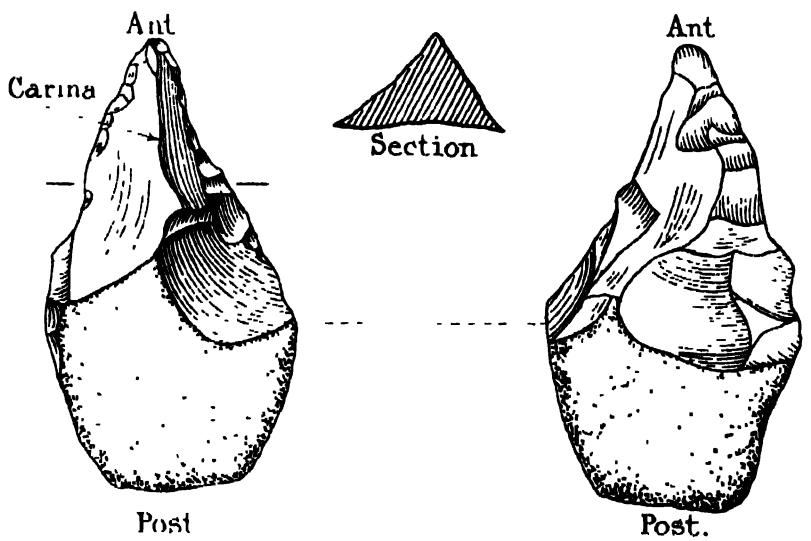



FIG. 15 (Somewhat reduced in size.)

a terrace-gravel of the Thames Valley, which has been made from a small nodule of flint, and the ventral surface of which has been flaked in the manner described. Fig. 16 illustrates an implement (also from the Thames Valley) of the same general type which has been made from one-half of a split nodule, and the ventral surface of which has been left unflaked. These and similar specimens have been known to archæologists as "flat-faced palæoliths," but this would seem to be an unsatisfactory title. They are in reality rostro-carinates in which the carina has become depressed, and it is of interest to note that their development from the ancestral form follows a similar course to the development of the skate from the squaloid fishes. This is shown

diagrammatically in fig. 17, and it will be seen to be quite different from the manner in which the plaice was developed (fig. 14), which method, as we have seen, approximates very closely to the development of the palæoliths of rhomboidal section, from the rostro-carinates. For these palæoliths with triangular section Sir RAY

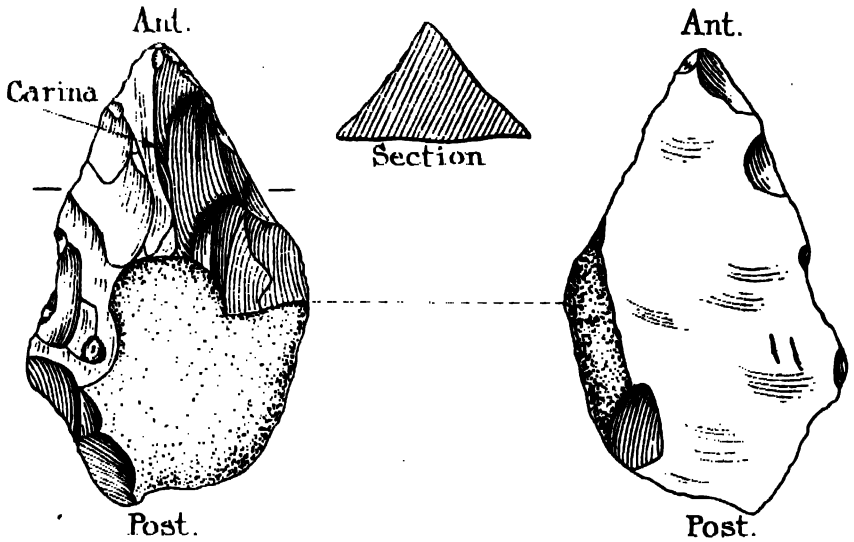



FIG. 16. (Somewhat reduced in size.)

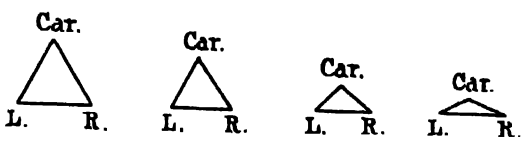



FIG. 17.

LANKESTER suggests the name "Batiform." Thus it seems that in the early palæolithic period two methods of implement making were in vogue, both intimately related to the manner in which the rostro-carinates were fashioned. The author has ascertained by experiment that the implements exhibiting a triangular section are more easily made than those of which the section is rhomboidal.]

## DESCRIPTION OF PLATES.

All Plates are reproduced from accurate drawings executed by Mr. LEONARD SQUIRRELL of Ipswich. The size of the figures on the Plates compared with the implements themselves is stated for each Plate. Four views of each implement are given as well as outline sections.

[*Note.*—All the specimens figured in the Plates, and in text-figs. 15 and 16, have been presented to the Department of British and Mediæval Antiquities and Ethnography of the British Museum, Bloomsbury.]

### PLATE 51.

(Actual size.)

Specimen recovered from gravel pit at Knowle Farm, Savernake, Wilts, by Rev. H. G. O. KENDALL, who presented it to the Author. Line of section indicated by vertical lines in fig. 1.

### PLATE 52.

(84/100 actual size.)

Another specimen from same gravel pit as above, also found and presented by Rev. H. G. O. KENDALL. Positions of sections indicated by vertical lines in fig. 1.

### PLATE 53.

(73/100 actual size.)

Specimen found 1893 in Odell's Pit, Dawley, near West Drayton, Midd., in the Thames Valley, by the late Mr. ALLEN BROWN. Line of section indicated as before.

### PLATE 54.

(84/100 actual size.)

From gravel pit at Warren Hill, Mildenhall, Suffolk, found by the late Mr. WORTHINGTON G. SMITH. Lines of the sections indicated as before.

### PLATE 55.

(Actual size.)

From gravel pit at Clapton, N.E. London, in the Thames or Lea Valleys. Found by the late Mr. GREENHILL. Line of section indicated as before.

PLATE 56.

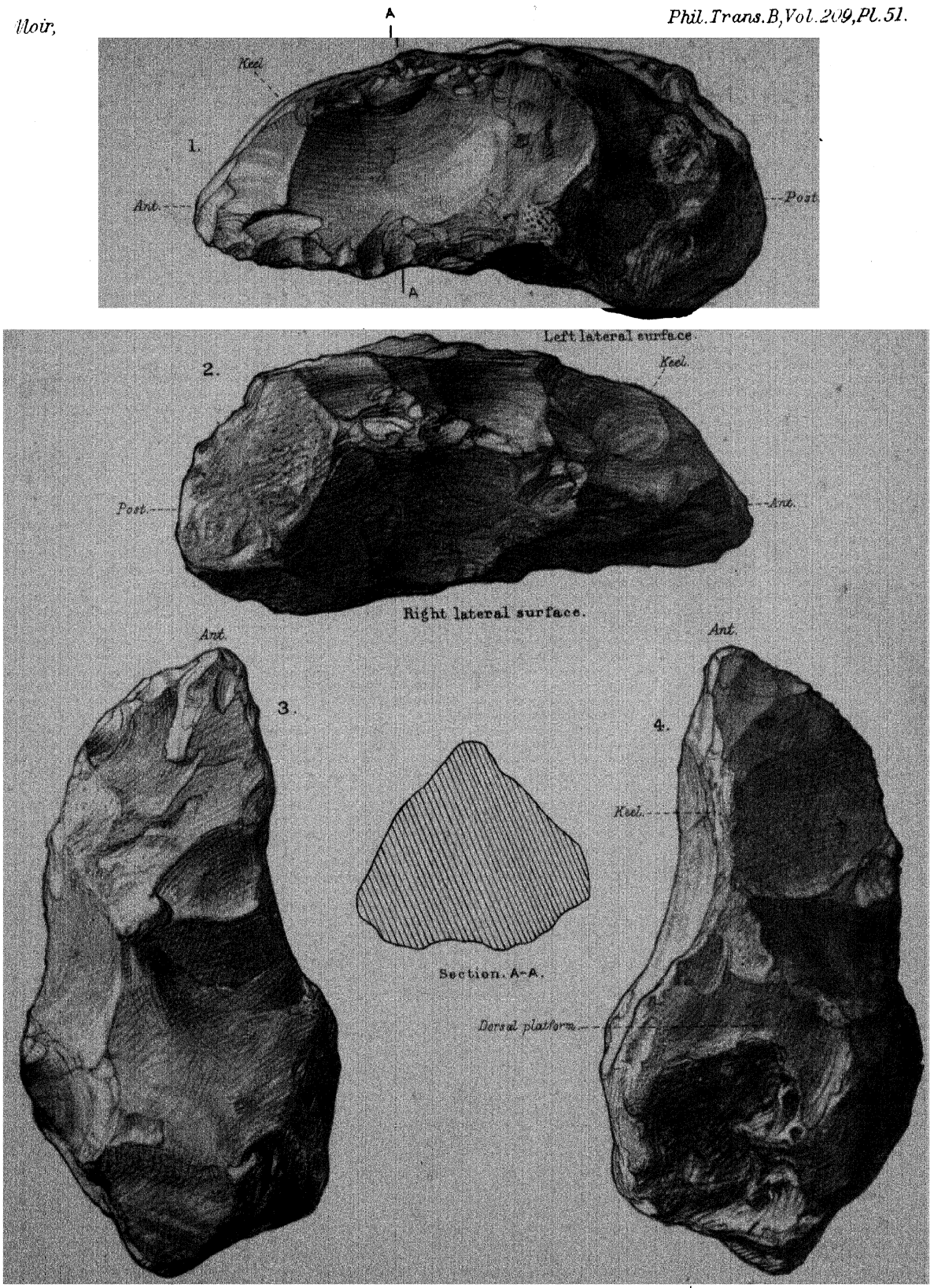
(Actual size.)

Found by a workman, employed by the author, in a gravel pit situated in a shallow valley on the plateau, east of Ipswich. Line of section indicated as before.

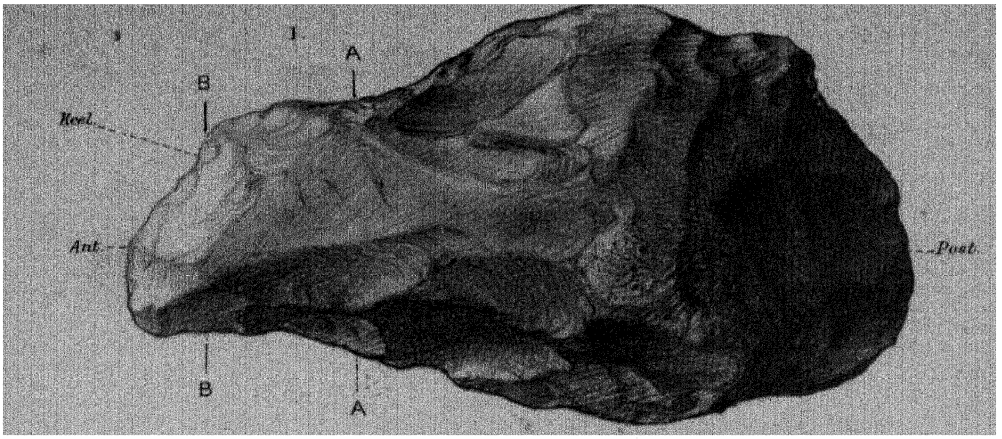
PLATE 57.

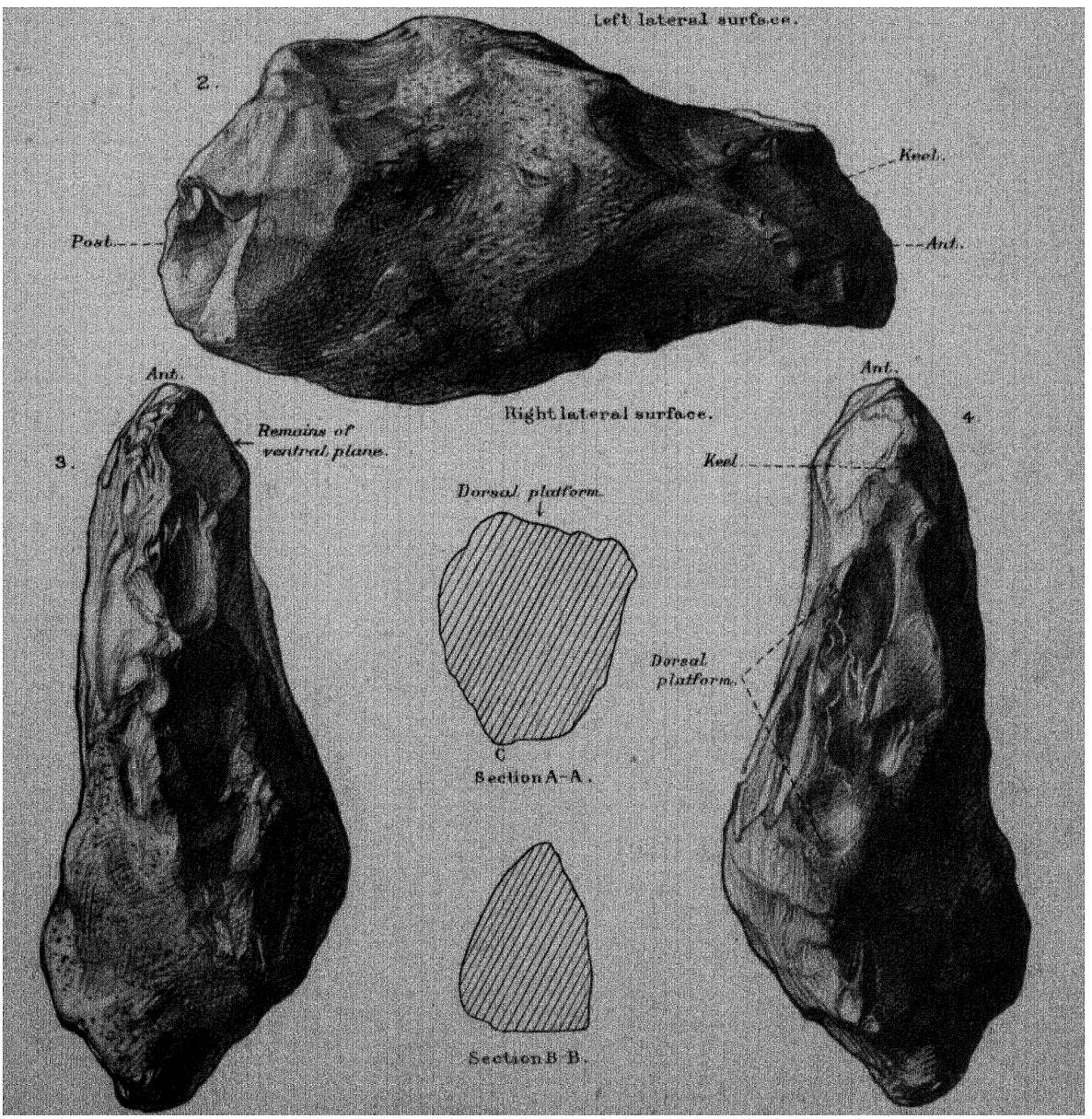
(84/100 actual size.)

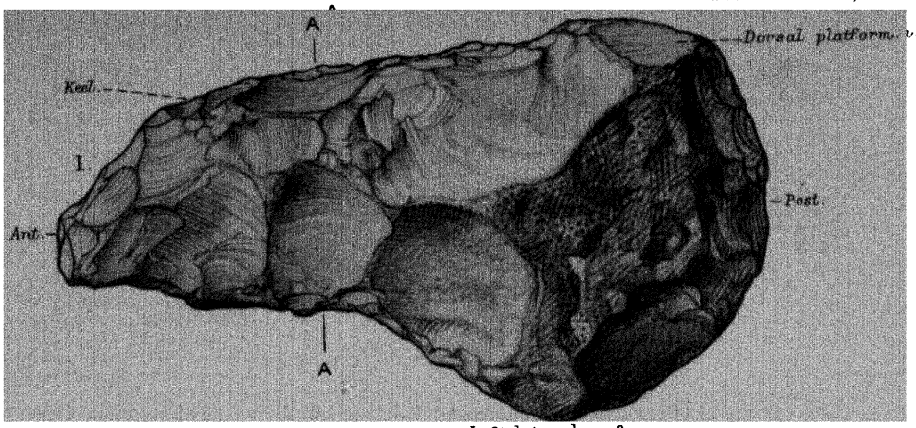
From gravel pit at Broom, near Axminster, Somerset. Presented to Author by Mr. A. S. BARNES. Line of section indicated as before.



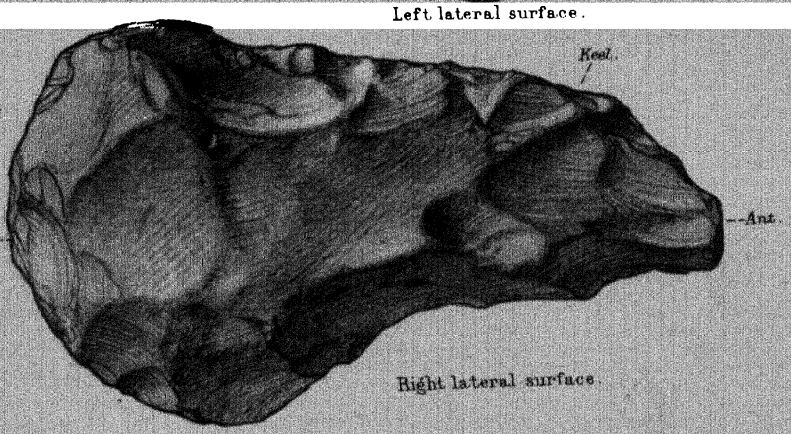

THE SAVERNAKE TRANSITIONAL, No 1.


1.
A
B
Keel.
Ant.
Post.
B
A


Left lateral surface.
2.
Keel.
Post.
Ant.
Ant.
Right lateral surface.
Remains of ventral plane.
3.
Dorsal platform.
C
Section A-A.
Section B-B.
Ant.
4.
Keel
Dorsal platform.
Post.
Ventral surface.
Post.
Dorsal surface.



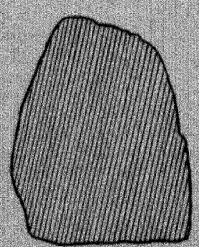

Left lateral surface.



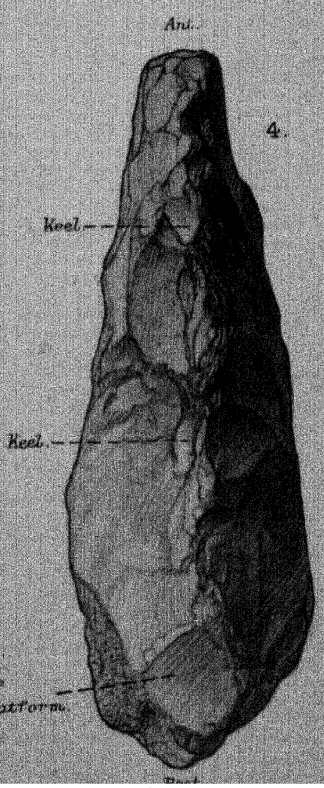

Right lateral surface.




Post.
Ventral surface.



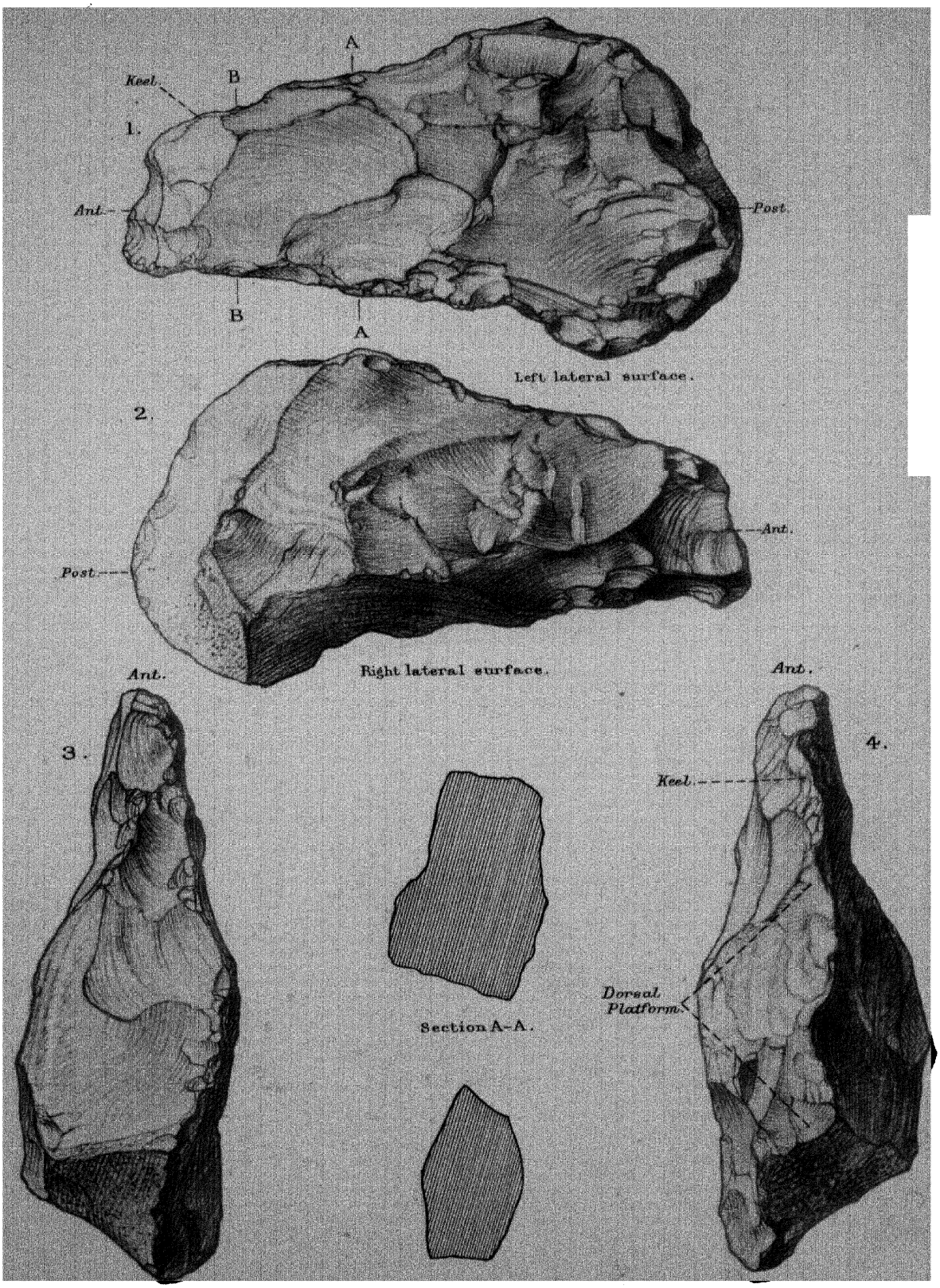
Section A–A.




Post.
Dorsal surface.

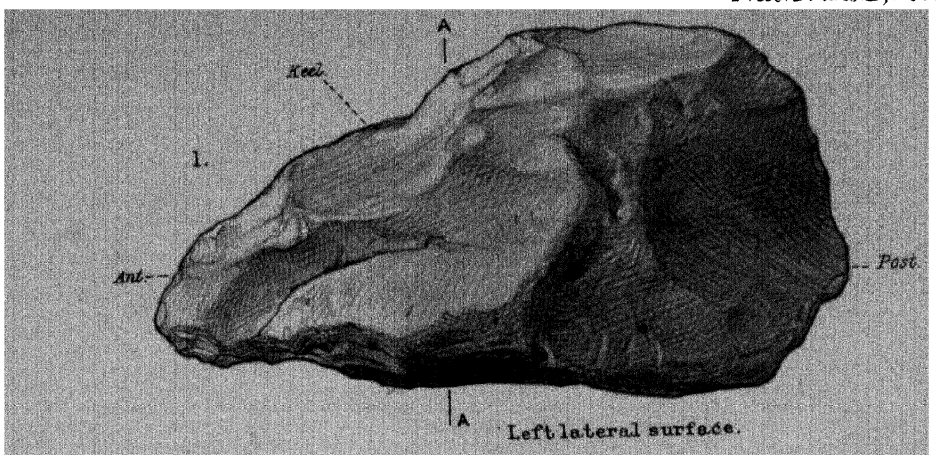
Huth coll.

THE DAWLEY TRANSITIONAL.

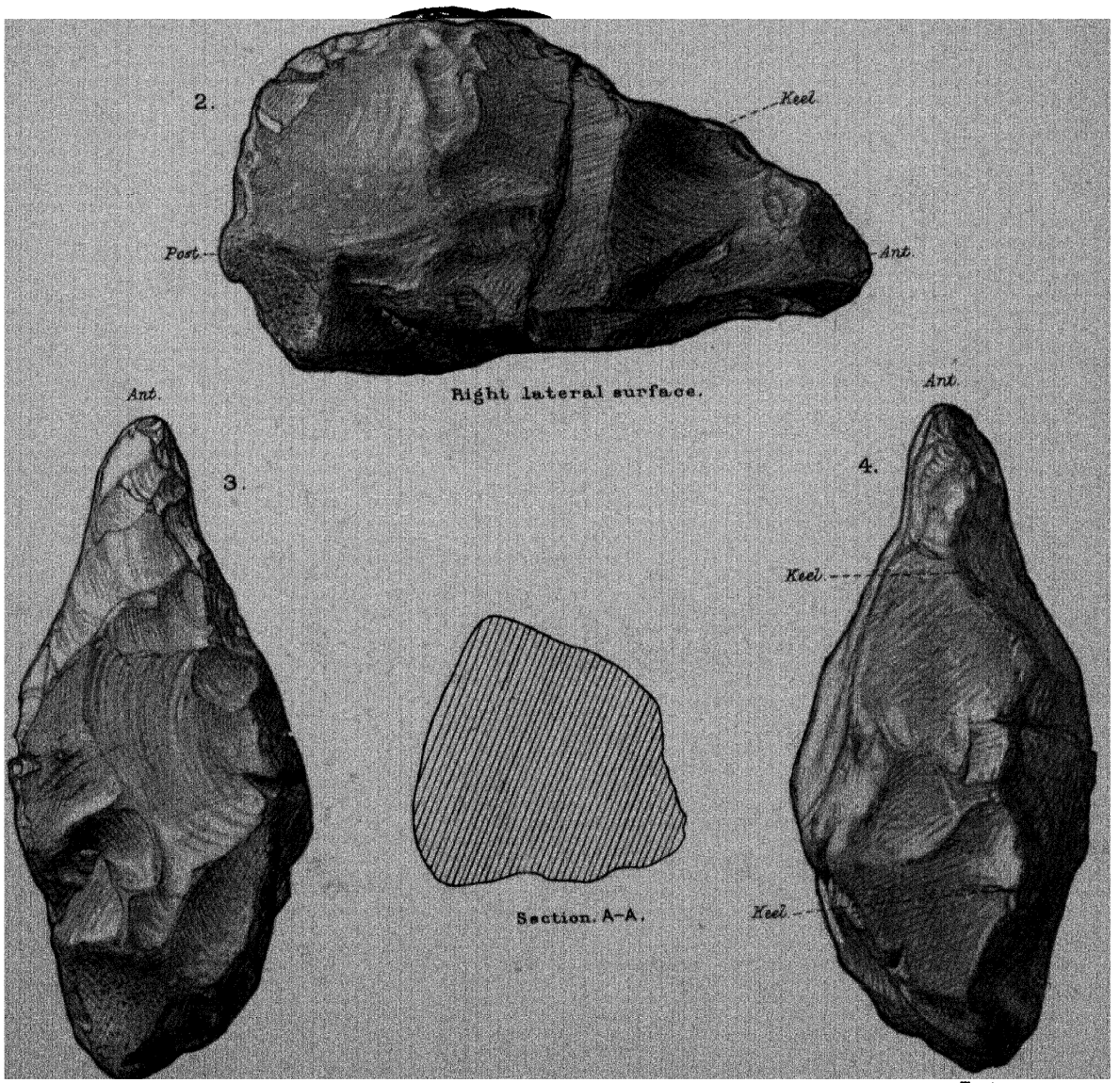



THE MILDENHALL TRANSITIONAL.

Huth coll.




Left lateral surface.




Right lateral surface.

*Post.*

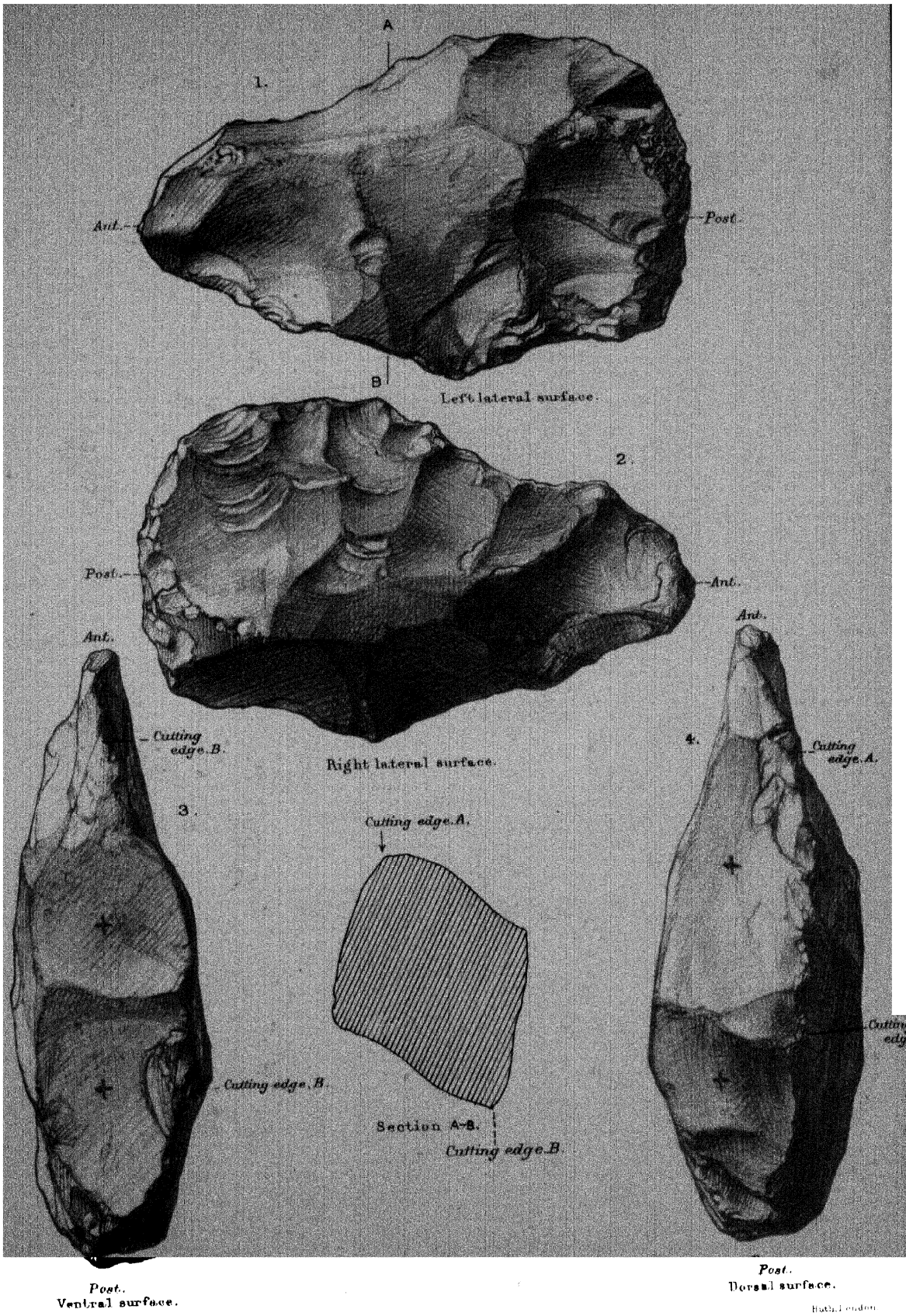
Ventral surface.

*Post.*

Dorsal surface.

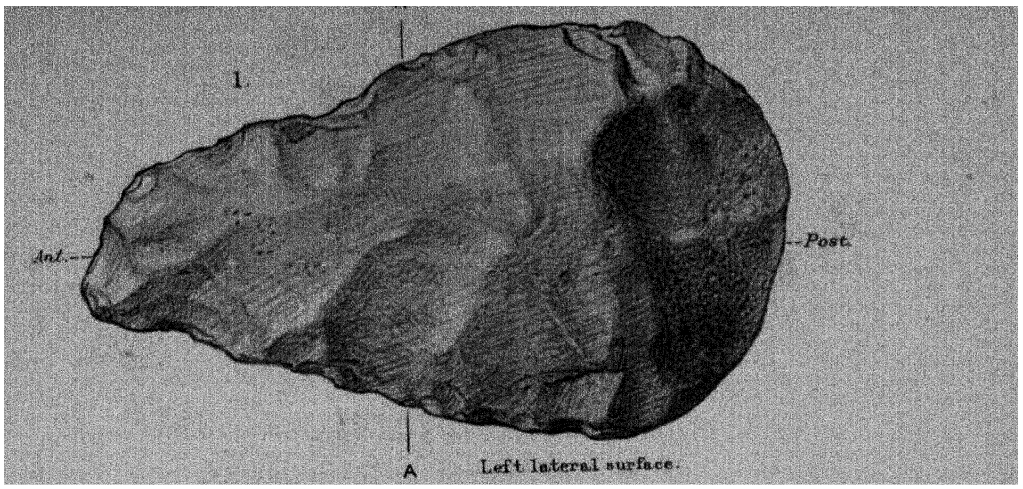
Huth coll

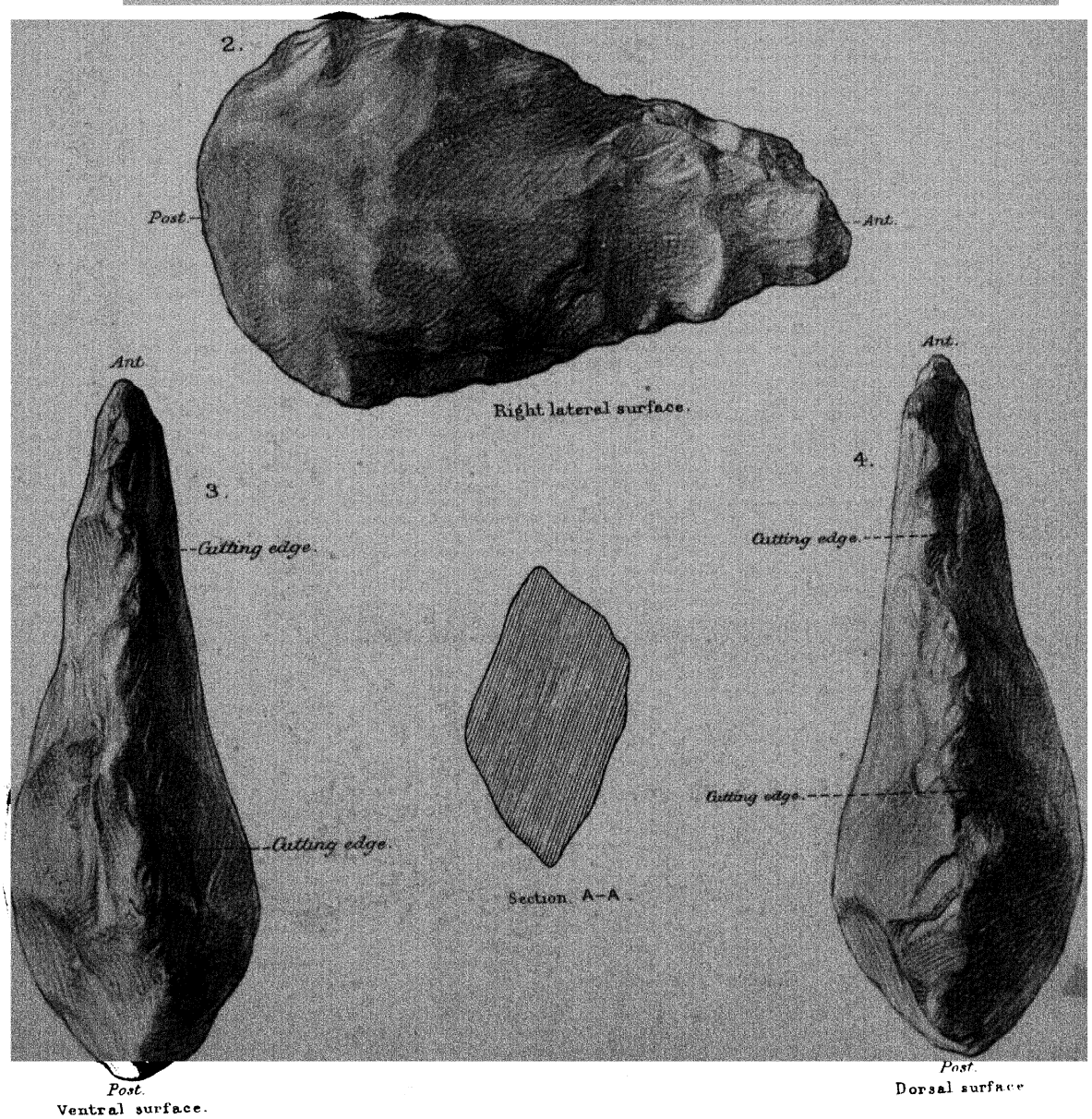
THE CLAPTON TRANSITIONAL.




THE IPSWICH TRANSITIONAL.

Phil. Trans. B, Vol. 209, Pl. 37.




THE AXMINSTER TRANSITIONAL.

# IX.—*The Development of the Sea-Anemones* Metridium dianthus (Ellis) *and* Adamsia palliata (Bohad).

*By* James F. Gemmill, *M.A., M.D., D.Sc.*

*Communicated by Prof.* E. W. MacBride, *F.R.S.*

(Received May 17, 1918,—Read June 27, 1918.)

[Plates 58–60.]

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*Metridium* and *Adamsia* are genera of the Family Sagartiadæ, Sub-Order Malacactineæ, Order Actiniidæ, Sub-Class Zoantharia. The Malacactineæ (or "True" Sea-Anemones) with the Scleractineæ (or "True" Corals) make up the Order Actiniidæ. In this Order there is an eight mesenteried Edwardsia stage, and thereafter a primary cycle of six couples of mesenteries is (or may be inferred to be) completed by the addition of two pairs to the eight Edwardsia mesenteries, while succeeding cycles are formed in the exocœles of the pre-existing mesenterial cycles.* Other so-called sea-anemones are the Zoanthidea and Cerianthidea, but, from the arrangement of their mesenteries, they have to be classed as separate Orders, though in all of them the primary Edwardsia mesenteries can be recognised during development or in the adult condition. The remaining Zoantharian Order, the Antipathidæ, is somewhat aberrant. Their development is unknown, but it is stated that one species, *Leiopathes glaberrima*, shows distinct indications of an Edwardsia stage.

## 1. Metridium† (Plate 58, figs. 1–24).

In this genus the column is long, cylindrical, smooth, naked, pierced by cinclides and ending in a capitulum which is divided into lobes and carries numerous short

* See Bourne, 3, p. 104.

† The generic name *Metridium* due to Oken is synonymous with, but has priority over, *Actinoloba* due to Blainville.

tentacles. A ring-like thickening surrounds the column below the capitulum. The sexes are separate and indistinguishable externally.

Having ascertained by microscopical examination that the ovaries of *M. dianthus* were full of *ripe* eggs in April, I made the necessary arrangements for stocking some of the research tanks at the Millport Biological Station with full-sized specimens from the piles at Kepel Pier, a short distance from the station. Two well-marked varieties occur together there, one flesh-coloured and the other white. A tank was reserved for each and two other tanks for crosses. As the eggs promised to be small even when full-grown, the outflow from each tank was drawn through a large fine meshed filter-drum immersed in the tank, so that they might not be swept away unobserved.

The first *spawning* was noted on June 5. The eggs proved to be heavier than water, and sank to the bottom, where they were seen without difficulty in contrast to the white glazing of the tanks. Filter drums were accordingly unnecessary at this stage. The eggs are opaque, 0·1 mm. in diameter, dark greyish-green in the white variety and brick red in the other. Development is the same in both.

Natural *fertilisation* readily occurred, a mutual stimulus to spawning being no doubt communicated by the sexual products. The same individuals spawned several times at longer or shorter intervals (2–10 days), and the last batches of eggs were extruded on July 10. I am much indebted to Mr. John Peden, laboratory attendant at the station, for helpful care in stocking the tanks, attending to eggs and larvæ, and preserving a full series of stages.

When spawning the anemones are usually well expanded, the stomodæum being partly everted and elongated in the axis of the siphonoglyphs. The eggs emerge not from the siphonoglyphs, but along the sides of the stomodæal aperture, being slowly swept out as if by the action of cilia there. (The cilia on the sides of the stomodæum act at times, if not continuously, as sweepers-out of the stomodæal cavity, *cf.* CARLGREN, 5.) The eggs are usually discrete from the first, but may be entangled for a time in fine strands of mucus, which soon dissolve away. *Maturation* appears to be advanced or completed just at the time of spawning, as none of the freshly-spawned eggs showed a germinal vesicle, while teased-out ovaries from resting specimens during the spawning season showed numberless full-sized ova, all with large germinal vesicles.

The ripe nucleus is invisible in the opaque egg-mass, but cleared specimens and sections show that it lies excentrically at a point about a third of the diameter of the egg inwards from the surface. The egg membrane is very thin, closely adherent, and unprovided with spines or other surface markings, or with a micropyle. The egg substance is finely granular, the granules being practically uniform in size and distribution, leaving only a very narrow clearer rind at the periphery.

Equal or subequal *segmentation* occurs. There is a tendency in some eggs for the inner ends of the daughter-cells to remain unseparated for a time, and in others for

the superficial furrows to be shallow and indistinct. Figs. 2, 3, 5 are photographs of typical stages showing complete segmentation.

A small central cavity appears at the 16-celled or even an earlier stage. As segmentation proceeds the cavity enlarges, sometimes directly and sometimes after preliminary formation of foldings of the blastula-wall (*cf.* pp. 356 and 360), which afterwards straighten out. The *blastula* cavities in the best broods (Plate 58, figs. 7, 9, 10) are devoid of other than fluid contents, but sometimes they contain cellular and non-cellular materials (Plate 58, fig. 8; Plate 58, fig. 20). In the best broods the wall of the blastula is formed of a single layer of cells, having the nuclei and most of the protoplasm near the surface, while the inner ends of the cells are yolky in character (*cf.* HAMMAR. 15). The cellular material above referred to includes segmentation cells, which have failed to arrange themselves alongside their neighbours in the blastula wall, and which may proliferate, while the non-cellular material consists of the inner yolky ends of blastula wall cells which have been constricted off (*cf. Adamsia*, p. 356).

The blastula begins to elongate in the future oral-aboral axis. From the first, the cells to one side of the segmenting mass have been slightly larger than the rest, and these cells now form a thickened patch at what will be the oral end. The end in question flattens and pushes inwards near its middle part, the larvæ becoming somewhat conical in shape. This marks the beginning of *gastrulation*. By further in-pushing (Plate 58, figs. 11-13) the gastrula stage is reached, the blastopore being now nearly, but not quite, in the middle of the somewhat truncated oral end. The blastopore has also become slightly elongated, one end (the future sulcar end, pp. 355, 363) being somewhat nearer the aboral pole than the other (*cf.* Plate 58, figs. 10, 13, 15). The former end has usually a less prominent lip or margin than the latter. In the earliest stages of gastrulation there is often cell-proliferation on the inner aspect of the in-pushing area, producing a small cap of additional endoderm, into which the archenteric cavity soon extends.

A short *stomodæum* is produced by early involution at the blastopore. It lengthens afterwards, mainly by interstitial growth. It shares in the elongation of the blastopore above described. Its cells may be distinguished from those of the archenteron by being closer set and more columnar, and by having longer and more deeply-staining nuclei. The archenteron cells form a less regular layer.

Also at the commencement of gastrulation some branched cells resembling "mesoderm" cells are given off from the endoderm into the blastocœle. A few flattened "mesodermal" cells are found later between ectoderm and endoderm.

*Swarming* begins in the early blastula stage, the movements being at first irregular but afterwards causing progression with the pointed (future aboral) end in front, together with rotation in the contra-solar direction, as viewed from that end. These movements persist through the planula stage, into which the late gastrula passes insensibly. Further elongation occurs: the shape becomes more cylindrical,

and the archenteron larger, while the blastula cavity is obliterated by approximation of hypoblast to epiblast. The stomodæum becomes longer.

The first two *mesenteries*, the future sulco-laterals (or ventro-laterals of authors) appear far ahead of the others, growing aboral-wards, each carrying on its free edge an extension of the stomodæal epiblast for the developing mesenteric filament. *Stinging cells* appear in the early planula, chiefly at its oral and aboral ends. Various acids readily cause extension of the stinging threads. (Plate 58, fig. 17.)

Towards the end of gastrulation a tuft of six or seven long rather stiff cilia grows out at the apex of the aboral pole from a small group of elongated columnar cells, and these cilia form a striking feature throughout the planula stage (*cf.* Plate 58, figs. 15, 22). When stretched out the cilia are half as long as the larva itself. They lie close together and are sometimes held straight, sometimes curving to one side or the other, as the larva progresses. Should the cilia encounter any obstacle, the larva quickly swerves. In the later stages the cells which carry the cilia sink slightly inwards, forming a small aboral pit, underneath which are a few branched cells. No doubt the whole forms an *aboral sensory* organ. Carlgren's (6) figure of the late planula of *Sagartia viduata* agrees with the above description. He adds that *Sagartia viduata*, *S. undata*, *S. troglodytes* and *Metridium dianthus* have practically identical larvæ.

Reference should also be made here to the aboral nervous elements described by McMurrich in *Rhodactis sancti-thomæ* (24), Appellöf (1) in *Actinia mesembryanthemum* and Duerden (9) in various Scleractinian larvæ and in *Lebrunia*.

The blastopore and stomodæal canal are not sealed up even temporarily, and indeed in the late planula are often opened as the creature swims along. *Ciliary feeding* occurs at this period. Foreign particles may be seen in the archenteron, and slight, though not great, increase of size occurs. Fine carmine grains are readily ingested. Carlgren (5) has shown that ciliary feeding almost certainly occurs in various adult Malacactineæ and in the Zoanthidea.

The gastrulæ and young planulæ swarm freely at all levels in the hatching vessels and will be swept away if there is a through circulation of water. The use of filter drums now becomes necessary in such vessels, but it is simpler to pipette the larvæ out into shallow separate dishes under aëration, and to change the water by pipetting them again into new dishes at intervals of a few days.

Older planulæ tend to remain at the bottom, moving horizontally and remaining stationary from time to time. Many of these now become temporarily *attached* to the bottom, *mouth downwards* (*cf.* Plate 58, fig. 24), the stomodæal canal everting itself to a varying extent and forming a sucker surface, now smaller now larger, permitting slow creeping movements to take place. I think it extremely probable that the larva is now feeding on such organic material as may be attached to the substratum.

Unfortunately I had to leave Glasgow in the beginning of July, just at the time

when the above stage was reached in my cultures, and on my return after some weeks the larvæ had disappeared, so I am unable to say how long the stage of creeping on the mouth may last, or to describe aboral fixation.

The sulco-lateral mesenteries early become edged by down growths of stomodæal ectoderm, for the *mesenteric filaments*. These are ciliated in the larva but I could not make out in what direction the cilia work. However in the smallest attached specimens of Metridium obtainable from the shore there is an aboral-ward current along the free borders of the mesenteries, and an oral-ward current along the outer walls of the gastro-vascular pouches. The early development and large size of the sulco-lateral mesenteries and their filaments suggest a comparison, from the physiological point of view, with the aboral ciliated bands which one finds in echinoderm and other larvæ, while the extension of ectoderm over endoderm which occurs in their formation is also paralleled in echinoderm development (see also p. 364).

In my latest larvæ, slight folds of hypoblast could be recognised near the oral end, foreshadowing the formation of the sulculo-lateral, sulcar, and sulcular mesenteries. Of these, so far as I could judge, the sulculo-laterals appear first, the sulcars next, and the sulculars a little later.

I have not been able to relate from direct observation the early somewhat excentric situation and the slit like shape of the blastopore to the position of particular mesenteries, but as Appellof (1) pointed out, this may be done with the help of Lacaze Duthiers' data for *Actinia mesembryanthemum*, the conclusion being that the shortest meridional line in the larva is at the future sulcar side (see p. 363). Duerden (9) notes also that in Scleractinian larvæ the blastopore has a slightly excentric position.

## II. Adamsia palliata (Plates 59–60, figs. 25–71).

The genus Adamsia belongs to the same family (Sagartiadæ) as *Metridium* (see p. 351). The characters of the genus are . . . all attached to movable objects: one or two girdles of cinclides on the column, each cinclide piercing a small tubercle: rest of column smooth: base secreting a cuticular membrane: a well-marked sphincter present: tentacles numerous.

The sexes are separate, and *spawning* in the Firth of Clyde lasts throughout September and the early part of October. Males and females are found in approximately equal numbers. Natural fertilisation regularly occurs a mutual stimulus to spawning being evidently operative, as in *Metridium*. The eggs are usually shed about midnight, but more timely spawning may be induced if the tanks are closely covered up to exclude all light in the early afternoon. This was done in order to secure quite freshly-spawned eggs at an hour more suitable for observing the earliest stages of development. Ripe males and females may, with difficulty, be distinguished from one another by taking the specimens out of water and noting the somewhat larger ridges caused by the fertile mesenteries on the surface of the female

in the collapsed condition. The same individuals spawn several times in each season. The Millport records show that spawning may also occur in early spring.

*Maturation* must take place immediately prior to spawning. Sections of ovaries with full-sized ova, even during the spawning season, show practically all the eggs still with a large germinal vesicle.

The eggs being somewhat lighter than water tend to float. They are opaque, spherical, 0·25 mm. in diameter. They vary as regards colour in different individuals from brick red to yellow, yellowish white, and white. The last two-named varieties have a peculiar glistening appearance. The ripe nucleus is invisible in the egg mass, but may be found in serial sections lying excentrically as in *Metridium* (p. 352). The great mass of the egg is made up of small yolk granules which are almost uniformly distributed, though not quite so closely packed near the centre of the egg. The egg membrane is thin, closely adherent, and unprovided with spines. Underneath it is an extremely narrow zone relatively free from granules (Plate 59, fig. 48).

After fertilisation the segmentation *nucleus divides* into two daughter nuclei, which in turn divide. Only when this second division is nearly complete is there the slightest indication of a commencing division of the egg mass into two by a cell wall beginning to form in the plane perpendicular to the axis of the first spindle. Immediately thereafter the second division of the cell mass can be noted as commencing, but the first and second *cell divisions* are completed at practically the same time, so that the first stage of external segmentation is the four-celled one. In this stage, the cells are equal in size and lie in one plane, their apposed surface being flattened against one another. An eight-celled stage supervenes, in which typically at first each cell lies directly against its sister-cell, so that the whole mass is quadrangular, but re-arrangement into the less regular grouping soon takes place. Four of the cells on one side of the mass are usually a little larger than the corresponding four on the other.

The succeeding divisions are sub-equal but irregular, giving rise to a *morula* which though at first roughly spherical in shape soon becomes extremely distorted by the formation of surface folds and ridges, always with a tendency to flattening in one plane. This may be called the *pre-blastula* stage (Plate 59, figs. 28–31; Plate 59, figs. 49–51).

Meantime, an irregular central cavity has appeared containing fine granules extruded from the cells (Plate 59, fig. 57). The result is to produce a thinnish crumpled disc made up of two sheets of cells separated by the cavity in question, which, however, is frequently of minute size. The crumpled disc gradually changes to a saucer-like shape by smoothing of the minor furrows and folding of the edges towards one side (Plate 59, fig. 32; Plate 59, figs. 52, 53). The saucer in turn becomes less spread out, but thicker-walled, and the cavity of the saucer gradually fills out, remaining, however, as a small dimple for a time (Plate 59, figs. 54, 55). Meantime, cell division has continued, the nuclei keeping near the external surface of the mass. The inner ends of the cells became prolonged as non-nucleated vesicles

surrounded by a protoplasmic wall and form a central reticulum of "*trophenchyme*" (Plate 59, figs 55 58).

The full *blastula* stage is reached by smoothing out of the last remains of the hollow of the cup, and commencing elongation. The shape is now oval, and one end, the end at which gastrulation will take place, soon becomes rather broader than the other. In the best broods the central reticulum is entirely devoid of nuclei, but in other cases nuclei may be present in larger or smaller numbers (Plate 59, fig. 56), and when present are derivatives of ectodermal cells at the bottom of a fold or of the saucer cavity, which did not succeed in ranging themselves with the rest on the outer surface. They are not the regular endodermal cells, and as far as I could judge are destined to break down and disappear, partly *in situ* and partly within the archenteric cavity, into which many pass later along with the central trophic material (trophenchyme) of the blastula (see below). Such relatively late stages as are illustrated in Plate 60, figs. 63–68, often show degenerating nuclei within the stomach cavity.

*Gastrulation* begins at the broad end of the larva (Plate 59, figs. 36 42, and Plate 59, figs. 60 62). This end becomes flattened, then pitted inwards, not in the middle, but usually a little to one side, so that the opening has a prominent lip opposite a retreating one (Plate 59, figs. 36–37). As in *Metridium* (p. 353) the blastopore is slightly elongated between the two lips named. The blastopore usually, but not always, coincides with the position of the former saucer opening. During the progress of gastrulation the central trophic material of the blastula gradually finds its way through the inpushing endoderm into the archenteron, which, in later stages, it fills with a loose reticulum often showing small nuclei in course of degeneration.

In view of the data given in the preceding paragraphs, I venture to suggest that in general the cell-contents of solid coelenterate planulæ with endoderm already formed need not be considered as wholly endodermal, but that part is a modified mesenchyme having a diffuse origin, and now "trophenchymal" in character. For a suggested explanation of its presence, see p. 365.

In some Adamsia larvæ the endoderm has to be described as arising partly by *unipolar* proliferation. The invaginating area becomes capped by a thicker or thinner mass of endoderm proliferated from its apex, and the archenteron extends into the middle of this mass, giving rise to the deepest portion of the gastric cavity. Whether any "mesoderm"* arises from endoderm during gastrulation proved impossible to decide.

A short *stomodæum* arises by involution at the blastopore, before gastrulation is completed, and subsequently increases in length by interstitial growth.

*Cilia* appears on the early blastula. At first it moves about irregularly, but when

* "Mesoderm" is used here, and on p. 353, to indicate middle layer cells proliferated from endoderm in the course of gastrulation.

elongation takes place the movement is a progression with the pointed (future aboral) end in front, combined with rotation in the sinistral or contrasolar direction. There is no special tuft of elongated cilia at the aboral end such as forms so marked a feature in the planula of *Metridium*. The gastrulæ and young planulæ tend to swim near the surface, but the older larvæ are found for the most part moving horizontally along the bottom of the hatching vessel, from time to time making upward excursions and then sinking down again. They are markedly elongated in the oral-aboral direction, and cleared specimens begin to show traces of the *mesenteric septa*, especially of the sulco-laterals (Plate 59, figs. 44 45).

Serial sections make it clear that of the eight primary mesenteries the two sulco-laterals are the first to appear, and for a long time are much the largest (*cf.* Plate 60, figs. 68, 71). They carry on their free surface a ridge of columnar ciliated cells for the future mesenteric *filament* which as in *Metridium* is a downward growth from the stomodæum (*cf.* Plate 60, figs. 64, 66, 67), and in the late larva extends to within a third of the length of the larvæ from the apex. The other mesenteries appear practically together, though it seemed that the sulcars (or ventrals of authors) and the sulculars (or dorsals of authors) were slightly later than the sulculo-laterals (*cf.* Plate 60, figs. 70 71). *Stinging cells* are already present over the larva as in *Metridium* (p. 354), but their distribution is more uniform.

The larva has now considerable power of elongation and contraction. *Fixation* by the aboral end next takes place, the larvæ being at first anchored loosely so that they can be detached by a current from a pipette. Soon, however, the attachment is firm and definite. This attachment must be by cement formation since there is no sucker to which it might be due. Fixation is followed by the throwing out of the eight *tentacles* (Plate 59, fig. 47), each corresponding to an intermesenteric space. These tentacles are not at first all of the same size. The four largest correspond respectively with the spaces between (*a*) the two sulcular mesenteries, (*b*) the two sulcars, (*c*) two laterals on either side. The smallest tentacles are the two between the sulculo-laterals and the sulculars.

Soon after attachment the *mouth* opens freely, and the body of the young anemone becomes elongated and cylindrical. It is still semi-transparent, allowing the ciliary currents inside to be watched. These are aboral-wards along the borders of the mesenteric septa and oral-wards along the sides and bottom of the inter-mesenteric spaces.

I failed to rear the anemones to further stages, and though they survived for several months, there was no great increase in size, and no new mesenteries or tentacles were formed. In fixation the larvæ attached themselves to glass, large sand grains, or small stones, but preference was given to fragments of dead mollusc shells, though not to shells carried about by tiny hermit crabs.

## III. Discussion.

(*a*) Ova, segmentation, blastula formation, p. 359.
(*b*) Origin of endoderm, p. 361.
(*c*) Formation of mesenteries and mesenteric filaments, p. 362.
(*d*) Phylogeny, p. 363.

(*a*) *Ova*, etc.—It may be of interest to bring together briefly such data regarding the eggs and early development of Malacactineæ as I can gather from the literature at my disposal or supply from observation.

*Size of ova.*—*Metridium dianthus*, 0·1 mm. in diameter; *Sagartia troglodytes*, 0·1 mm.; *Metridium marginatum* (McMurrich, 24), 0·1 mm.; *Adamsia palliata*, 0·25 mm.; *Urticina crassicornis*, 0·6 mm.; *Bolocera tuedia*, about 1·1 mm.; *Peachia hastata*, judging from a figure by Faurot (10), 0·25 mm.; *Anthea cereus*, 0·35 mm. It will be seen that the largest eggs in the list (those of *Bolocera*) have more than 1000 times the capacity of the smallest (those of *Metridium*).

*Egg membrane.*—Smooth in *Metridium dianthus*, and *M. marginatum* (McMurrich, 24), *Adamsia palliata*, *Sagartia troglodytes*: with characteristic spines in *Urticina* (Appellöf, 1), *Peachia* (Faurot, 10), *Actinia mesembryanthemum* (Lacaze Duthiers, 19), *Bolocera tuedia*, and *Anthea cereus*.

*Cell contents.*—Finely granular with practically uniform distribution of granules, *Metridium dianthus*, and *M. marginatum* (McMurrich, 24), *Adamsia*: granular with the granules distributed in zones and mixed with clear vesicles most abundant centrally, *Urticina crassicornis* (Appelloef, 1), *Bolocera tuedia*.

*Micropyle.*—Present in *Urticina*: absent in *Metridium dianthus*, and *M. marginatum* (McMurrich, 24), and *Adamsia*.

*Segmentation.*—Equal or subequal segmentation is the rule. The segmentation is total from the first in *Metridium dianthus*, and *M. marginatum* (McMurrich, 24), *Peachia* (Faurot, 10), *Sagartia parasitica* (Kowalewsky, 18, and Faurot, 10), *Actinia bermudensis* (Cary, 7), *Cerianthus*.* Cleavage of the cell mass is delayed till after more than two daughter nuclei have risen from the segmentation nucleus (four in *Adamsia*, sixteen in *Urticina crassicorni* (Appellöf, 1), more than sixteen in *Bolocera tuedia*. It should be added that, in *Adamsia*, Appelloef (1) and Faurot (10) speak of the occurrence of a two-celled stage, but such a stage is entirely exceptional in my experience. It may be noted that, among Alcyonarians, the eggs of *Alcyonium digitatum* undergo total cleavage from the first (Matthews, 29), while those of *Renilla* (Wilson, 34) take the course characteristic of *Urticina* and the Arthropods. McMurrich describes secondary loss of cell partitions as sometimes occurring in *Metridium marginatum* (24). I have not been able to satisfy myself that this takes place in *M. dianthus*, but, on the other hand, it

* See Delage (8), p. 676.

is not uncommon, though atypical, for the early divisions to be incomplete, and to leave the inner ends of the cells confluent (*cf.* Plate 58, fig. 6).

*Blastula formation.*—Blastula formation is at its simplest in *Metridium*, following the course taken, for example, by the developing eggs of an ordinary sea-urchin (*Echinus esculentus*) or starfish (*Asterias rubens*). However, in *Metridium* the yolk of the blastosphere cells is aggregated towards their inner ends, and there is a tendency in atypical cases for the yolky parts to become separated off as non-nucleated fragments into the central cavity, as well as for nucleated cells derived from the original morula mass to be present there and to proliferate. Similar cells are frequently found in the central cavity of abnormally developing sea-urchin and starfish blastulæ. As in *Metridium*, they are not concerned with the formation of the proper endoderm, but ultimately break down and are absorbed, unless they are present in sufficient quantity to interfere with the growth and differentiation of the larvæ. The occurrence of analogous cells in the central trophic reticulum was sometimes noted in *Adamsia*, where they were found in greatest numbers just internal to pre-blastula folds, and, in particular, to the remnant of the saucer opening.

*Adamsia* exhibits in a most striking manner these peculiar *foldings* of the pre-blastula, which have now been found to precede the full blastula stage in many different forms, *e.g.*, *Cribrella* (Masterman, 27), *Solaster* (Gemmill, 11), *Porania* (Gemmill, 12), *Luidia* (Mortensen, 30), *Cucumaria* (Newth, 31), *Alcyonium* (Matthews, 29), and, in a minor degree, *Metridium*. Such foldings were already noted in *Adamsia* by Faurot (10), and we may infer from a remark by this author that they are characteristic of *Cerianthus* as well. They are not referred to by Appellof (1) in his description of the development of *Urticina crassicornis*, but I find that they occur very markedly in this species, as well as in *Bolocera tuediæ*. It is a curious circumstance that the *Adamsia* pre-blastulæ commonly take on a saucer or cup-like shape during the stage in question. Probably the cause is a mechanical one, depending on the interaction of two processes, viz., the straightening out of the pre-balstula folds and the separation of the central trophic reticulum described on p. 357 and referred to below.

*Formation of central trophic mass.*—Appellöf, in *Urticina* (1), first gave an adequate description of the manner in which this mass arises, namely, by constriction of the inner, usually non-nucleated ends of the cells of the morula and pre-blastula. In the immediately succeeding stage this author shows the blastosphere cells definitely separated off from the central mass. The feature in question is not found in *Adamsia*, where the inner ends of the blastosphere cells remain continuous with the strands of the central reticulum till near the end of gastrulation. Probably the formation in the blastula of a non-nucleated or sparsely nucleated trophic central mass is a characteristic feature of Actinian development, except in such species as *Metridium dianthus* and *marginatum*, where the eggs are minute and

have little yolk. At any rate, we have now detailed accounts of the origin of the central trophic mass in *Urticina* and *Adamsia*, and, from the descriptions of FAUROT (10), KOWALEWSKY (18), and APPELLÖF (1), we can infer the likelihood of similar processes occurring in *Adamsia parasitica*, *Peachia hastata*, *Cerianthus*, *Bunodes*, and *Actinia mesembryanthemum*. They occur markedly in *Bolocera tuediæ*. A phylogenetic explanation is suggested on p. 365.

(b) *Endoderm Formation.*— Both in *Metridium* and *Adamsia* the endoderm arises by invagination, sometimes accompanied by unipolar cell proliferation, and the developing archenteron is hollow. In *Metridium*, the blastula cavity being empty, the process is uncomplicated. In *Adamsia* the in-pushing endoderm allows the central mass to pass gradually through into the archenteric cavity, without losing continuity as a layer. APPELLÖF (1) was the first to describe this process in Actinian development (*Urticina crassicornis*).

I am unable to accept MCMURRICH'S conclusion (26) that endoderm formation takes place by delamination in *Metridium marginatum*. This species is closely allied to *M. dianthus*, with which it agrees in the general character of the ova and in the details of segmentation and blastula formation. MCMURRICH'S description and figures do not testify to the presence of nuclei in those portions of the blastosphere cells which he believes are separated off to produce the hypoblast. His view is based rather on not having secured evidence of invagination than on having secured evidence of delamination. I can only infer that his material was deficient in the early stages of gastrulation, and possibly also that some of it showed the abnormal features referred to on p. 353, and illustrated in Plate 58, figs. 20, 21, of this paper.

We can now say with some confidence that gastrulation is the general rule in Malacactinian development. Apart from *Metridium* and *Adamsia*, it has been described in *Urticina* (1), and *Actinia bermudensis* (CARY, 7), *Actinia mesembryanthemum* (JOURDAN, 17), *Cerianthus*, and an Actinian allied to *A. mesembryanthemum* (KOWALEWSKY, 18). To these I am now able to add *Bolocera tuediæ*. The case appears to be different in Alcyonarians, where delamination is described by WILSON (34) in *Renilla* and MATTHEWS (29) in *Alcyonium digitatum*. Again, in the Scleractinian *Manicina*, WILSON (35) states that transverse division of the blastosphere cells takes place, giving rise to a coarsely granular endoderm, but this is very like the mode of formation of the central trophic mass in Malacactineæ.

Embolic gastrulation, which occurs also in the Scyphozoa, is almost certainly the type from which such modes of endoderm formation as epibole in Siphonophores and Ctenophores, and unipolar immigration in various Hydromedusæ, are proximately derived. However, in view of the "regulatory" potencies exhibited by the blastomeres and blastula-fragments of *Adamsia*,* it seems entirely probable that cells proliferated or nipped off into the interior, normally or pathologically, from any

* See p. 366 and *cf.* ZOJA'S (36) results for various Hydromedusæ.

part of the blastula surface, will strive to become endodermal *in functional imitation of* invagination endoderm, and, under suitable circumstances, may succeed. Experimental embryology shows that potencies of structure-formation which, under normal circumstances, have been acquired and are exercised only locally, may become part and parcel of the heredity of the whole layer to which the structure belongs. Witness lens formation on the skin of amphibian larvæ over transplanted optic vesicles.

*Supplementing or supplanting* of gastrulation-endoderm by endoderm of multipolar or of diffuse ingressional origin might thus gradually take place in the history of particular stocks, families, and even genera. It involves no inconsistency to hold that gastrulation is the primary method of endoderm formation in coelenterates, and yet to recognise that the other methods named have become fixed as normal for particular forms. Surely the *polarity* between ectoderm and endoderm could never have been established except through the formation of a digestive cavity, which sank in from the surface, and opened on the surface from the first.

(c) *Formation of mesenteries.*—It has long been recognised that a stage with eight primary mesenteries (Edwardsia stage) in characteristic bilateral symmetry, forms an important landmark in Zoantharian growth. *Metridium* and *Adamsia* furnish additional illustrations of the definiteness of this stage. In *Metridium* the two sulco-lateral (or "ventro-lateral" of authors) mesenteries appear far ahead of the others, and they have probably a current-producing function in the late larva (p. 354). The same pair has a similar but less marked priority of origin in *Adamsia*. Lacaze Duthiers (19) in *Actinia mesembryanthemum*, Faurot (10) in *Halcampa*, and McMurrich (24) in *Rhodactis sancti-thomæ* and Duerden (9) in Scleractinian larvæ also describe the sulco-laterals as being the first to appear.

In *Metridium* the sulculo-laterals next become evident. Then follow the sulcars (ventrals of authors), and the sulculars (dorsals of authors), the latter, as far as I could judge being slightly later than the former. This is the sequence described by McMurrich (24) for *Rhodactis sancti-thomæ*, and by Faurot (10) for *Halcampa*, but Lacaze Duthiers (19) in *Actinia mesembryanthemum* gives the sulculars as second, the sulcars as third, and the sulculo-laterals as last in the order of appearance, though as Haddon suggests, his work needs revision by serial section methods. *Adamsia* seems to agree with *Metridium*, *Rhodactis*, etc., though there is little difference as regards the three pairs of mesenteries in question. In the heavily yolked eggs of *Urticina*, with presumably abbreviated development, Appellöf (1) described the eight mesenteries as arising at much the same time or without regular sequence, though the sulco-laterals seemed to show a certain priority. I can add that this priority is definite in *Urticina crassicornis* at Millport, and that the sulculars are the last to be formed.

The primary gastro-vascular pouches are naturally eight in number, and two of them, the sulcar and the sulcular, lie in the axis of bilateral symmetry. The eight

first tentacles correspond in position with the pouches. In the Scleractinians (DUERDEN 9, WILSON 35, and others) the eight primary mesenteries arise in the same order as in *Metridium* and *Rhodactis*.

The evidence from *Metridium* and *Adamsia* appears quite definite that the mesenteric *filaments* consist of (or at any rate include) a stomodæal epiblastic downgrowth in the case of the sulco-laterals. Probably the same thing is true as regards the other mesenteries, though their filaments had not yet developed in my oldest specimens. This agrees with the general trend of recent evidence on the question in the *Actiniidæ*.

(d) *Phylogeny*.—Whatever may be conjectured about the primitive cœlenterate planula, the balance of embryological evidence tends to show that the *intermediate* planula for Scyphozoa and Anthozoa, was a hollow free-swimming digestive bag with a single opening—originally the blastopore of an embolic gastrula—and a tendency to the formation of radially arranged mesenteries and gastric pouches.

I venture to suggest that while the Scyphozoa remained essentially free swimming, except for purposes of asexual reproduction, and preserved or perfected their radial symmetry, the Anthozoa (as well as the Turbellarians, and probably also the higher Metazoa) had, as their *proximate* ancestral form, a larva which took to creeping mouth downwards and gathering food material from the substratum, thereby acquiring an ectodermal stomodæum for the ingestion of food, and increasing their mesenchyme for body movements. If the larva took to moving in a particular direction the mouth might naturally become elongated in that direction and other rudiments of bilateral symmetry be acquired. The aboral sense-organ would also shift forward. Hints of this stage may be seen in the slit-like character and excentric position of the blastopore in Actinian larvæ (p. 355), one end of the slit being nearer the aboral pole than the other. That nearest the aboral pole would naturally mark the "head" end of the creeping planula. Similar features carried afterwards to full bilaterality and principal-axis formation are recognised as occurring in Turbellarian ontogeny (LANG, 20).

As regards the Zoantharia it appears to me legitimate on these lines to amplify for the Edwardsia stage the suggestion (made by VAN BENEDEN (2) for *Cerianthus*) that the arrangement of the gastro-vascular pouches corresponds with the arrangement of the *cœlomic pouches* in the higher segmented forward-moving animals. This view takes, as necessary foundations, SEDGWICK'S (33) well-known homology between gastro-vascular pouches and endodermal cœlomic outgrowths, and his comparison of mouth and anus with the two ends of an elongated primitive mouth, the middle part of which became closed.

As APPELLÖF (1) pointed out in the case of *Urticina*, it would appear from a comparison of Actinian larvæ with the early growth stages of *Actinia mesembryanthemum* described by LACAZE DUTHIERS (19), that what is called above the "head" end of the blastopore opening is to be identified with the sulcar side

of the Actinian stomodæum. We may accordingly institute the following comparison of the gastro-vascular pouches in the Edwardsia stage common to all Zoantharia; (1) The sulcar pouch corresponds with an (unpaired) præoral cœlomic cavity; (2) the pouch on either side between the sulcar directive mesenteries and the sulco-laterals with a (paired) collar cœlomic cavity; (3) that on either side between the sulco-laterals and the sulculo-laterals with a (paired) first trunk cœlomic cavity; (4) that between the sulculo-laterals and the sulcular directives with a (paired) second trunk cœlomic cavity; and (5) that between the sulcular directives with a third (unpaired) posterior trunk cœlomic cavity.

The comparison ceases here for most of the Zoantharia, since after the Edwardsia stage, increase in the number of pouches takes place by subdivision of already existing ones. However, in *Cerianthus* if, as seems certain, the orientation given by VAN BENEDEN (1), DELAGE (8), FAUROT (10), BOVERI (4), and MCMURRICH (26) be right, there is, as VAN BENEDEN (2) pointed out, continuous production of new pouches at the sulcular or "posterior" end, thus providing a striking resemblance to cœlom formation in such an animal as Amphioxus.

The sulco-lateral mesenteries of the late Actinian larva (*cf.* Plate 58, figs. 18-19) divide the archenteron into a smaller cavity (on the sulcar side) which may be taken as representing the "anterior" pouch of the hypothetical tetramerous cœlenterate ancestor (MASTERMAN, 27) and a larger cavity (on the sulcular side) which will represent for a time the other three pouches of the ancestor. Assuming that the primitive cœlenterate mouth lengthened and closed medially to form the definitive mouth and anus, the sulco-lateral representatives would probably be found commencing in the floor of the mouth much in the position of the *endostyle rudiment* of Amphioxus* and Tunicates, and of the ventral ciliated band of Tornaria, and of the V-shaped part of the adoral ciliation in echinoderm larvæ.

These structures are related to a primitive and always necessary function, the ingestion of food, as are the sulco-laterals of a planula of *Metridium*.

The characteristic position of the *muscle banners* on the mesenteries of a young Zoantharian might be explained as suitably meeting the needs for protraction and retraction respectively of the "body" and "head" in the creeping ancestor. The need for separation of out-going and in-going currents (respiratory or nutritive) in any large fixed cœlenterate would ensure the retention of bilaterality once acquired.

Colony formation with elongation of the mouth in relation to the axis of an

* A parallel to *chorda formation* from endoderm is found in cœlenterates. One may note that young *Pleurobrachia pileus* are much stiffer along their meridional lines than over the rest of their surface. Sections show that the outer walls of the meridional canals consist in great part of large vacuolated cells presenting a remarkable resemblance to developing notochordal tissue, and that there are two similar but smaller "stiffening" strips in the wall of each paragastric canal where it abuts on the stomodæum. The presence and distribution of vacuolated cells in Ctenophores has, of course, long been known, but in view of the question above referred to, it seems opportune to cite this instance of their close affinity to chorda tissue as regards differentiation and function.

elongated stock, has been put forward by HAACKE (13) as the originating cause of Hexactinian bilaterality, but this explanation seems altogether far-fetched.

When the Zoantharian stock became fixed, a kind of *metamorphosis* would occur, allowing a reduction of the mesenchyme needed in the free condition. A similar reduction might indeed accompany fixation in any coelenterate. This mesenchyme might be utilised for nutritive purposes as occurs, for example, in the metamorphosis of Echinoderms. Reflected forward in present ontogeny the reduction process might furnish a starting-point for the peculiar formation of the *trophenchyme* (pp. 357, 360), and for its passage into or inclusion within the archenteron, and its digestion there. Even in the late metamorphosis of Echinoderms the nutritive material derived from lost larval structures finds its way to the stomach, the walls of which for a time become syncytial and greatly thickened (see *e.g.*, MACBRIDE, 22, GEMMILL, 11). Information regarding the early development of the Zoanthidea would be of much interest since the adults have abundant mesenchyme.

BOURNE (3, and p. 19 of Ctenophora) expresses the view that "the Turbellaria, Nemertines and Ctenophora are descended from a common ancestor," which "would be spherical or hemispherical in shape, and have an aboral sense-organ consisting of a plate of thickened ectoderm provided with long stiff cilia. The line joining mouth and sense-organ would be the chief axis of the body. The digestive tract would consist of a stomodæum and a more or less sacculated endoderm, and would be surrounded by a mesenchymous tissue derived from a special germ layer, the mesoblast. Such an ancestor would itself be . . . very probably a form resembling the early larvæ of Actinians."

The above conditions are strikingly fulfilled in the planula of *Metridium*, except that the "mesoderm" (see p. 353) is too scanty to be called a layer.

It may be added against the hypothesis which derives Turbellarians from Ctenophores (1) that the branched canals (mainly ectodermal, but probably also partly endodermal), characteristic of various Zoanthidea with abundant mesenchyme (HADDON, 16) offer a better comparison with the Platyelmian excretory system than do the aboral tubes of Ctenophores, and that, as SEDGWICK pointed out, marginal pores in Medusæ and cinclide perforations in Actiniæ may be compared with nephridial openings; (2) what is known regarding the development of the Platyctenian Ctenophores indicates that they are modified from distinctively Ctenophoran forms; (3) the Ctenophore-Turbellarian hypothesis risks the initial danger of deriving a lowly phylum from a greatly specialised prototype; (4) the eight ciliated lobes of Müller's Turbellarian larva have an arrangement with reference to the axis of bilaterality which corresponds to that of the eight tentacles of a young Actinian and not to that of the ribs and meridional pouches of Ctenophores; (5) lastly, the resemblance between a *Metridium* larva creeping mouth-downwards (p. 354) and a Turbellarian claims consideration.

## IV. Abnormalities.

*Double Monsters.*—Several of these reached fixation and tentacle formation in my hatching vessels. In all the base was single. In one specimen a larger erect column carried a smaller one coming off at right angles from it near the base. In others the division was more equal and occurred quite near the crown or at a varying distance down the column. In perfect cases the two heads had the full number of tentacles and mesenteries. One triple monster was noted. In this case a column, single at the base, was divided into two, and of these one was again divided. The first head and one of the two other heads were perfect, while the third had only four or five tentacles. A mouth opening was present in each of the three heads. A certain number of young larvæ with two or even three gastrula-invaginations appeared in my early cultures, and there can be no doubt that as in *Luidia* (Gemmill, 13), the double and triple *Adamsia* monsters developed from such abnormal larvæ.

*Experimental.*—Separation of single blastomeres in the 4- and 8-celled stages of *Adamsia*, and fragmentation of the preblastula in the same species occur readily when the eggs are shaken. The isolated cells or cell masses tend to develop further, giving rise to tiny swarming larvæ with a mouth and gastric cavity. One late specimen, which had probably developed from a blastomere of the 4-celled stage, when cut into sections showed the two sulco-lateral mesenteries with their stomodæal epiblastic downgrowths. Many Cœlenterates exhibit passage of chromatin from the nucleus into the protoplasm and yolk of the growing ova. This process occurs in *Adamsia*, and accordingly we have an argument against the localisation of organ-building substances being necessarily connected with it.

*Irregularities of mesenteries.*—Apart from double and triple monsters, I came across no late larvæ which varied from the typical 8-mesenteried bilateral symmetry. We may be certain therefore that out of the hosts of young *Metridium* which one finds in suitable localities, a grain of wheat and upwards in size, very few have grown directly from attached planulæ. Examination of their mesenteries gives only the rarest instances in which the arrangement could be derived from a typical 8-mesenteried stage, and comparison of specimens indicates how readily regeneration from a portion of the base containing only a few mesenteries takes place. I have seen a slender specimen ($\frac{3}{8}$ inch long) with only five tentacles and the same number of mesenteries. Healing, formation of a new mouth, and gradual production of new mesenteries occur with great readiness. This kind of reproduction takes place in the Firth of Clyde most abundantly among the small anemones which find attachment to masses of mussels in the lower tidal zone. Perhaps wave action, the irregularity of the spaces between the shells, often bridged by byssus threads, and the sharp edges of the shells may give a greater mechanical stimulus to division than is experienced by anemones living in a smoother and more settled environment.

The process is not so much one of budding as of fragmentation, and this may

explain the remarkable irregularities which have been recorded in the mesenteries of various species of Malacactineæ. Thus PARKER (32) states that out of 131 adult specimens of *Metridium dianthus*, 77 had one, 53 had two, and one had three siphonoglyphs. There is no need to suggest with PARKER that such monoglyphic and diglyphic specimens may be different varieties, or with MCMURRICH (25) that a pair of originally directive mesenteries may have become non-directive. PARKER himself refers to the possibility that his irregular specimens may have arisen as buds, while MCMURRICH (25) pointed out the absurd situation which would arise if classificatory importance were to be attached to the monoglyphic, or even to the aglyphic, condition taken by itself. PARKER'S tryglyphic specimen may have originated from a double monstrosity. We had living at Millport a good-sized double *Metridium*, dredged near the Station, and showing no change whatever for several years, except increase in size. Numerous references to double Anemones occur in literature, and these are usually described as stages in ordinary fission, but I am convinced that stable duplicity of developmental origin may occur in Actinians, as it does in so many other types of animals.

## V. SUMMARY.

*Segmentation* is equal or subequal, total from the first in *Metridium*, beginning with a 4-celled stage in *Adamsia*. There is a bilaminar, greatly folded, and subsequently often saucer-shaped *pre-blastula* stage in *Adamsia*. The blastulæ are spherical, hollow in *Metridium*, but filled in *Adamsia* by a central *non-nucleated* or *sparsely nucleated trophic mass*, produced by constriction of the inner yolky ends of the blastula wall-cells. *Embolic gastrulation*, sometimes assisted by unipolar cell proliferation, occurs in both, and in *Adamsia* the central trophic material gradually passes through the in-pushing endoderm into the cavity of the archenteron. In *Metridium* a small amount of "mesoderm" is formed from the developing endoderm cells. The blastopore becomes the mouth, and in early stages is oval or slit-like and slightly to one side. The larva of *Metridium* has an *aboral tuft* of long cilia and an aboral *sense-organ*. The *stomodæum* forms by in-folding of epiblast at the blastopore, with subsequent elongation by interstitial growth. There is a definite 8-*mesenteried* stage. The sulco-lateral mesenteries are the first to appear. The *mesenteric filaments* contain down-growths of stomodæal epiblast. The planula is provided with stinging cells. In *Metridium*, prior to aboral fixation and to tentacle formation, *creeping*, mouth-downwards, with stomodæum more or less everted, occurs. Probably *feeding* takes place at this time, as it does during the immediately preceding late planula stage. It is suggested that the Anthozoa acquired an ectodermal stomodæum, and the rudiments of bilateral symmetry during a creeping ancestral stage, from which also the Turbellaria and the Higher Metazoa were derived (p. 363, *et seq.*). The Turbellaria, however, are nearer to the primitive Zoantharian than to the Ctenophoran type (p. 365).

A close comparison is made between the series of primary mesenteric pouches in Edwardsia and the cœlomic pouches of higher segmented animals (p. 363, *et seq.*). A distinction is drawn between trophenchyme and endoderm in the cell-contents of solid cœlenterate planulæ, and a phylogenetic explanation of the presence of the former is hazarded (p. 365). Double monstrosity, irregularities of mesenteries, and production of larvæ from isolated blastomeres or from blastula fragments, are briefly discussed (p. 366).

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## EXPLANATION OF FIGURES.

All the illustrations, except Figs. 22–24, are photomicrographs of sections, or of specimens mounted whole.

### Abbreviations Employed.

*ab. cn.*, aboral pole with stinging threads extruded; *bl.*, blastopore; *bl. c.*, blastula cavity; *ect.*, ectoderm; *end.*, endoderm; *g. c.*, gastric cavity; *mes.*, mesoderm; *nuc. tr.*, nuclei in trophenchyme; *o. cn.*, oral pole with stinging threads extruded; *s.*, a developing mesentery; *s. l.*, sulco-lateral mesenteries; *s. l. f.*, sulco-lateral mesenteries showing epiblastic down-growth from stomodæum for mesenteric filament; *s.* 2, sulculo-lateral mesenteries; *s.* 3, sulcar (*future* sulcar directive) mesenteries; *s.* 4, sulcular (*future* sulcular directive) mesenteries; *s. c.*, saucer cavity; *s.g. c.*, segmentation cavity; *s. or.*, aboral sense-organ; *st.*, stomodæum; *st.* 1, *st.* 2, stomodæa of a double specimen; *st. ep.*, epithelium of everted stomodæum; *tr. bl.*, trophenchyme within the blastula; *tr. g.*, trophenchyme within the archenteron or gastric cavity of the planula.

### Plate 58 (*Metridium*).

Fig. 1.—Egg of *Metridium* recently shed. The small adherent body may be a polar corpuscle.

Fig. 2.—Two-celled stage.

Fig. 3.—Four-celled stage.

Fig. 4.—Stage with ten cells. The cells here are more widely separated than is usual.

Fig. 5.—Section of corresponding stage (normal) in which the cells are closer.

Fig. 6.—Sections of early stages. In the right-hand specimen the cells are incompletely separated from one another at their inner ends (see p. 352).

Fig. 7.—Section of early blastula. The central cavity is slightly larger than is usual at this stage. It will be noted that, here and in fig. 9, the yolky contents are chiefly aggregated towards the inner ends of the cells.

Fig. 8.—Section of later blastula showing cellular and non-cellular contents in the blastula cavity (see p. 353).

Fig. 9.—Section of typical fully formed blastula. The thinner-walled slightly swollen region is the future aboral end.

Fig. 10.—Section of blastula showing commencing invagination of the entoderm. The shape has now altered, the aboral end being more pointed than the oral one.

Figs. 11, 12.—Sections of slightly later stages in gastrulation, the first chosen as showing a very narrow invagination cavity, while in the second the cavity is more widely patent. Separation of a few cells from the inner aspect of the in-growing part is seen in both cases. These cells are interpreted as being "mesodermal" in character.

Fig. 13.—Section of later gastrula. A cell thickening is seen at the aboral end the rudiment of the aboral sense-organ.

Fig. 14.—Longitudinal section of a young planula.

Fig. 15.—Longitudinal section of older planula showing the apical tuft of cilia and the cell thickening underneath it. The stomodæum is an open canal. In figs. 12–15 the early tendency for one lip of the blastopore to be slightly more prominent than the other is exhibited.

Fig. 16.—Longitudinal section of similar planula showing one of the long sulco-lateral mesenteries with its border of ectoderm derived by down-growth from the stomodæum.

Fig. 17.—View of planula mounted whole, showing the oral and aboral armature of stinging cells with the threads shot out. The aboral end is uppermost, and the dark line down the middle is caused by the thickened sulco-lateral mesenteries.

Fig. 18.—Transverse section through upper part of gastric cavity of late planula showing the large sulco-lateral mesenteries which divide the cavity into a larger and a smaller compartment.

Fig. 19.—Transverse section through middle part of gastric cavity of similar planula showing the developing sulco-lateral mesenteries as slight inward projections.

Fig. 20.—Sections of early blastulæ containing in their central cavities a greater than normal amount of cellular and non-cellular material.

Fig. 21.—Attempt at gastrulation in a larva having its central cavity filled with cellular and non-cellular material. These larvæ, while abnormal, may be of interest as throwing light on the mode of entoderm formation in certain other species which do not exhibit a hollow blastula stage.

Fig. 22.—Diagram of longitudinal section of larva (at stage represented in fig. 16), passing through the sulco-lateral mesenteries on either side, and showing also the stomodæum and gastric cavity. The downward extension of stomodæal epiblast on the surface of the mesenteries is indicated by the black line.

Fig. 23.—Diagram of transverse section through upper part of gastric cavity of a slightly older specimen than that shown in fig. 18. The black line on the surface of the sulco-lateral mesenteries (*s.* 1) marks the downward extension of stomodæal epiblast. The first indication of the sulculo-lateral (*s.* 2), the sulcar (*s.* 3), and the sulcular (*s.* 4) mesenteries is also shown.

Fig. 24.—Diagram of the late larva, in longitudinal section, at stage of oral fixation and creeping. The stomodæum is everted, bringing the oral ends of the sulco-lateral mesenteries into contact with the substratum.

PLATE 59, Figs. 25–62; (*Adamsia*).

Fig. 25.—Egg immediately after shedding.

Fig. 26.—Four-celled stage (3 hours).

Fig. 27.—Early morula (5 hours).

Fig. 28.—Later morula (characteristically irregular; photographed as an opaque object; 10 hours).

Fig. 29.—A group of morulæ, pre-blastulæ and blastulæ (photographed as opaque objects; 6–30 hours).

Fig. 30.—Pre-blastula (crumpled disc) stage under higher magnification (15 hours).

Figs. 31, 32. Early saucer pre-blastula stages (the latter photographed as an opaque object; 18 hours).

Figs. 33.—Late saucer stage; the remnant of the saucer cavity is seen faintly in the centre being now almost completely filled up (24 hours) (*cf.* figs. 54, 55).

Fig. 34.—Typical smooth blastula (photographed as an opaque object).

Fig. 35.—Late blastula with flattening at one end where gastrulation will take place. In this specimen the small notch on the right side still marks the remnant of the saucer opening. The darker central area is non-nucleated trophic reticulum (30 hours) (*cf.* fig. 60).

Figs. 36, 37.—Commencement of gastrulation (30–36 hours). The prominent lip of the blastopore (see p. 357) is on the left side in fig. 36, and uppermost (*i.e.*, towards the microscope) in fig. 37.

Fig. 38.—Stage similar to the last two (36 hours), but still showing remnant of saucer opening as a slight dimple (photographed as an opaque object).

Figs. 39–42.—Stages in gastrulation (48–72 hours).

Fig. 43.—Fully formed planula (84 hours). There is marked elongation: the stomodæum is still relatively short.

Fig. 46.—Older larva (4½ days) in side view with oral extremity at upper side of figure. The dark streak down the middle is caused by one of the two sulco-lateral mesenteries.

Fig. 45.—Similar stage viewed from oral end and focussed so as to show the two sulco-lateral mesenteries projecting inwards.

Fig. 46.—Slightly older stage (six days), viewed from oral end and focussed so as to show the eight primary mesenteries.

Fig. 47.—Young anemone (a week after fixation : 13 days) with the eight tentacles expanded.

Fig. 48.—Section of freshly spawned egg showing the finely granular contents, rather clearer in the centre. The thin egg membrane is slightly separated at several points.

Fig. 49.—Section through early morula showing some flattening and formation of a central cavity.

Fig. 50.—Section through slightly later morula (10 hours) showing irregularity of outline.

Fig. 51.—Section through an early pre-blastula (15 hours), crumpled disc stage.

Figs. 52, 53. –Sections through similar or slightly later (18 hours) pre-blastulæ in which the edge of the bilaminar disc is upturned all round in cup- or saucer-like form.

Fig. 54.—Section through late pre-blastula (24 hours). Filling up of the saucer cavity and formation of the central trophic reticulum are in progress.

Fig. 55. –Longitudinal section through a blastula (30 hours) in which the last-named processes are practically completed, only a slight dimple on one side remaining to mark the former position of the saucer opening. The central trophic reticulum in this specimen, as in the best blastulæ, contains no nuclei.

Fig. 56.—Transverse section of a blastula of similar age (30 hours), showing a group of nucleated corpuscles near its centre (see p. 357).

Figs. 57, 58.—Portions of sections of pre-blastula (18 hours) under medium and higher magnification, illustrating mode of formation of the central trophic reticulum. Clear vesicles, with a wall of protoplasm but without nuclei, are being partially separated off from the inner ends of the cells and pushed into the central cavity, which in this case is relatively large.

Fig. 59.—High power view of portion of blastula at stage shown in fig. 55. The nuclei are all near the free surface, the deeper zone being non-nucleated trophic reticulum.

Fig. 60.—Longitudinal section of late blastula (36 hours). The commencement of gastrulation is indicated by flattening of one end with proliferation and in-pushing of cells there.

Fig. 61.—Early stage in gastrulation (48 hours). The cavity of the archenteron gradually fills up with the trophic material which passes through the hypoblast from the interior of the blastula (×120). (The section does not pass quite through the apex of the aboral pole.)

Fig. 62.—Middle stage in gastrulation (64 hours), showing elongation of the larva and further sinking in of the archenteron.

PLATE 60 (Figs. 63–71) (*Adamsia*).

Fig. 63.—Longitudinal section of late planula showing stomodæum and gastric cavity. The surface of the larva is covered with shot-out stinging threads.

Fig. 64.—Longitudinal section of similar stage. The section passes along the whole length of the epiblastic (mesenteric filament) edge of the two sulco-lateral mesenteries.

Fig. 65. --Transverse section of planula at same stage as fig. 64, the section passing through the main portion of the gastric cavity. The trophic material of the larva is now inside the gastric cavity.

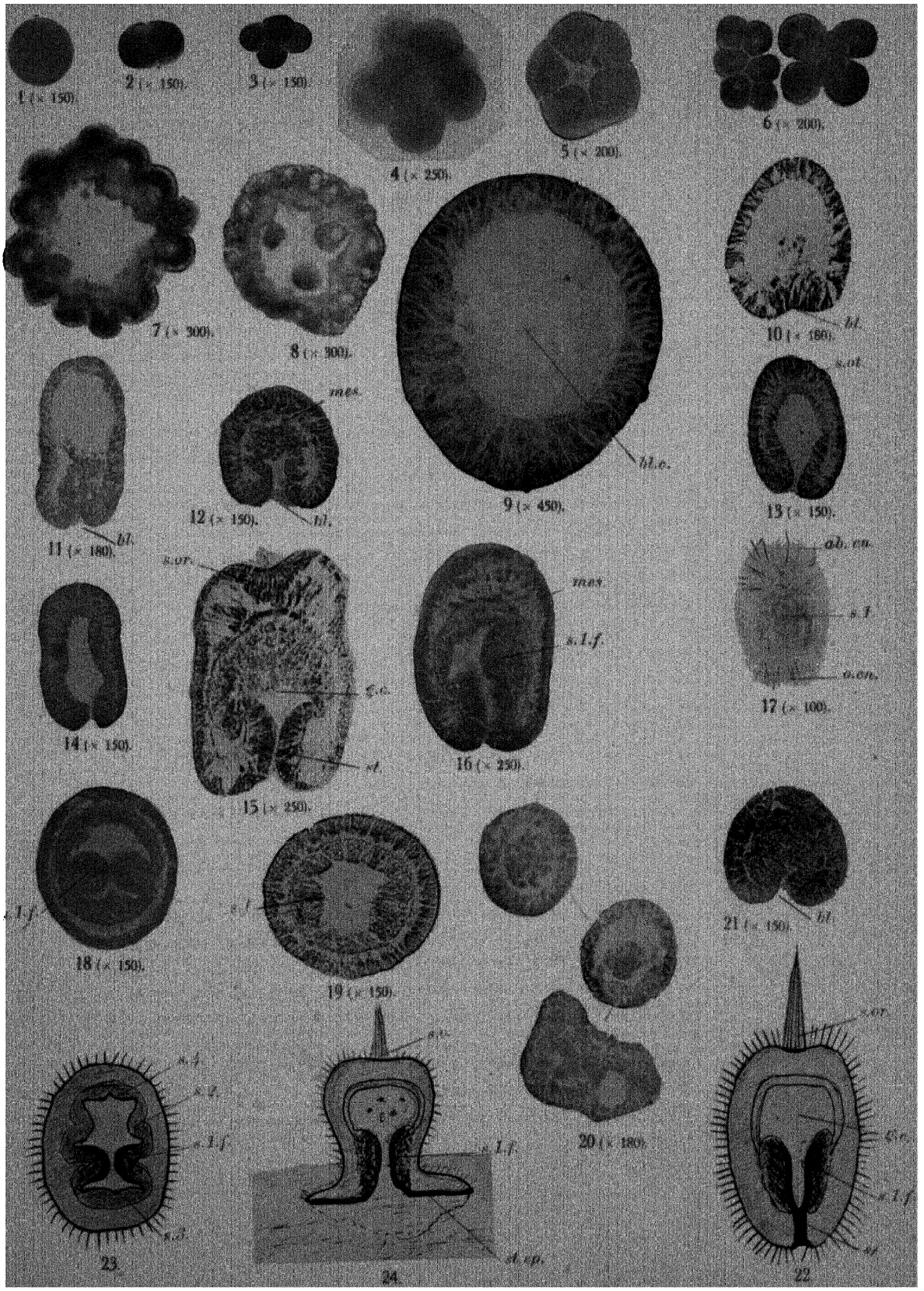
Fig. 66.—High power view in longitudinal section of oral end of a larva at time when down-growth of stomodæal epithelium to form a mesenteric filament is in progress. This down-growth is seen on the right side of the figure, the mesentery concerned being a sulco-lateral one. On the left side the section passes only through stomodæum.

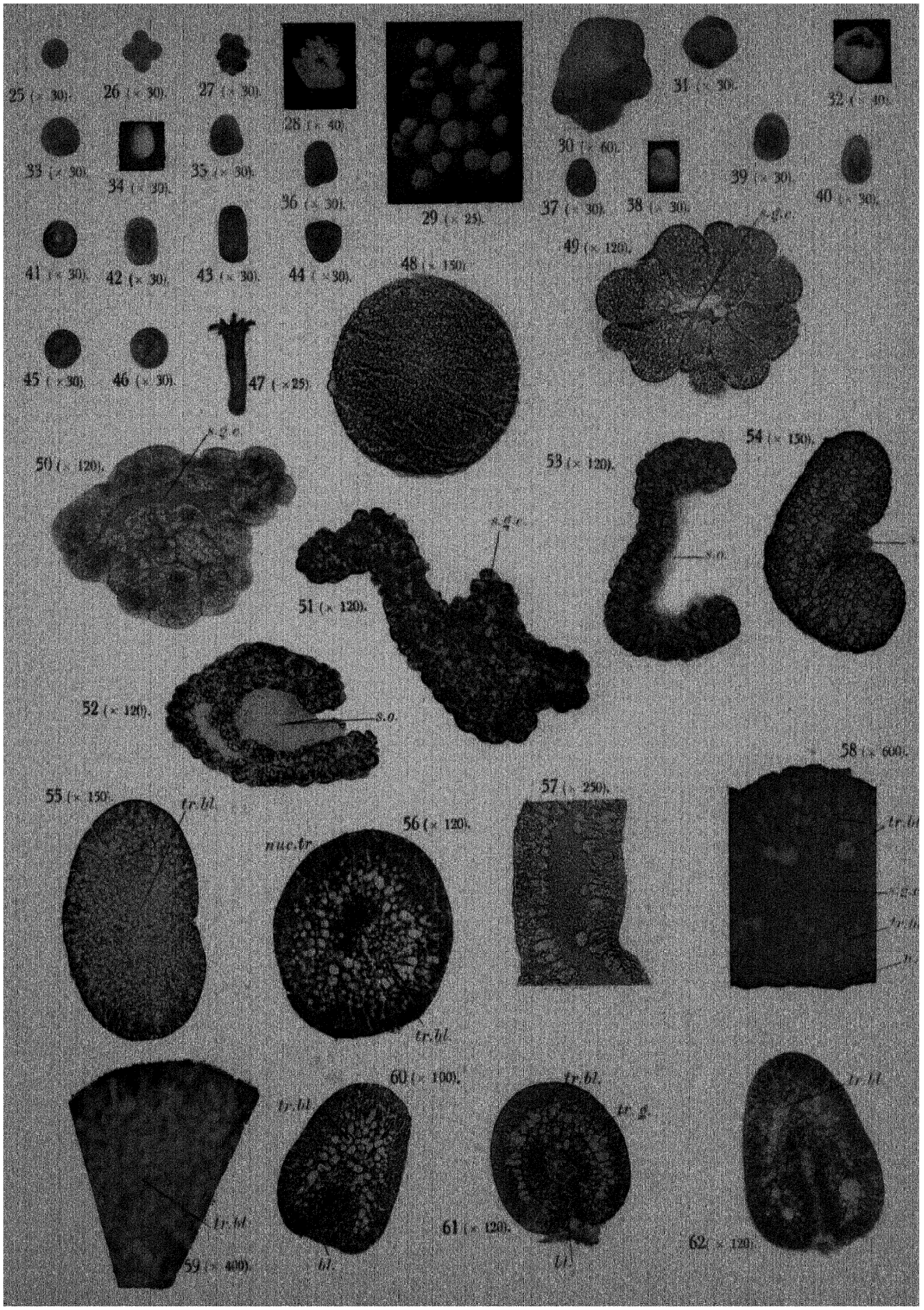
Fig. 67.—Almost longitudinal section of late larva ready for attachment. The superficial involution at × is not stomodæum but part of the future peristomial area tucked in owing to contraction of the larva when brought into the preserving fluid. On the right side of the figure, one of the sulco-lateral mesenteries with the mesenteric filament border from the stomodæal epiblast is cut along its whole length; on left side of figure the section cuts stomodæum and gastric cavity only.

Fig. 68.—Transverse section through gastric cavity of a larva slightly younger than that shown in fig. 66. The central trophic material, the two sulco-lateral mesenteries, each with a mesenteric filament border, and rudiments of other developing mesenteries are shown.

Fig. 69.—Aboral end of a larva similar to the stage illustrated in fig. 67, seen in longitudinal section. The greatly elongated ectoderm, the irregular entoderm with nuclei at various depths, and the fibrillar couch containing a few mesodermic nuclei between ectoderm and entoderm are shown. Fibres, probably muscular and sensory, from this couch are seen passing out into the ectoderm.

Fig. 70.—Transverse section near oral end of an attached stage (*cf.* Plate 59, fig. 47), showing the eight primary mesenteries. A little higher up in this series (*i.e.*, nearer the mouth), the sulcular mesenteries are complete like the rest.


1 (× 150).
2 (× 150).
3 (× 150).
4 (× 250).
5 (× 200).
6 (× 200).
7 (× 300).
8 (× 300).
9 (× 450).
10 (× 180).
bl.
11 (× 180).
bl.
12 (× 150).
mes.
bl.
bl.e.
13 (× 150).
s.at.
14 (× 150).
s.or.
15 (× 250).
s.c.
at.
16 (× 250).
mes.
s.l.f.
17 (× 100).
ab. en.
s.l
o.en.
18 (× 150).
s.l.f.
19 (× 150).
s.l
20 (× 180).
21 (× 150).
bl.
23.
s.l
s.l.
s.l.f.
s.d.
24.
s.c.
s.l.f.
al.ep.
22.
s.or.
s.c.
s.l.f
az


25 (× 30).
26 (× 30).
27 (× 30).
28 (× 40).
29 (× 25).
30 (× 60).
31 (× 30).
32 (× 40).
33 (× 30).
34 (× 30).
35 (× 30).
36 (× 30).
37 (× 30).
38 (× 30).
39 (× 30).
40 (× 30).
41 (× 30).
42 (× 30).
43 (× 30).
44 (× 30).
45 (× 30).
46 (× 30).
47 (× 25).
48 (× 150).
49 (× 120).
s.g.c.
50 (× 120).
51 (× 120).
52 (× 120).
s.o.
53 (× 120).
54 (× 150).
55 (× 150).
tr.bl.
56 (× 120).
nuc.tr.
57 (× 250).
58 (× 600).
59 (× 400).
60 (× 100).
bl.
61 (× 120).
tr.g.
62 (× 120).

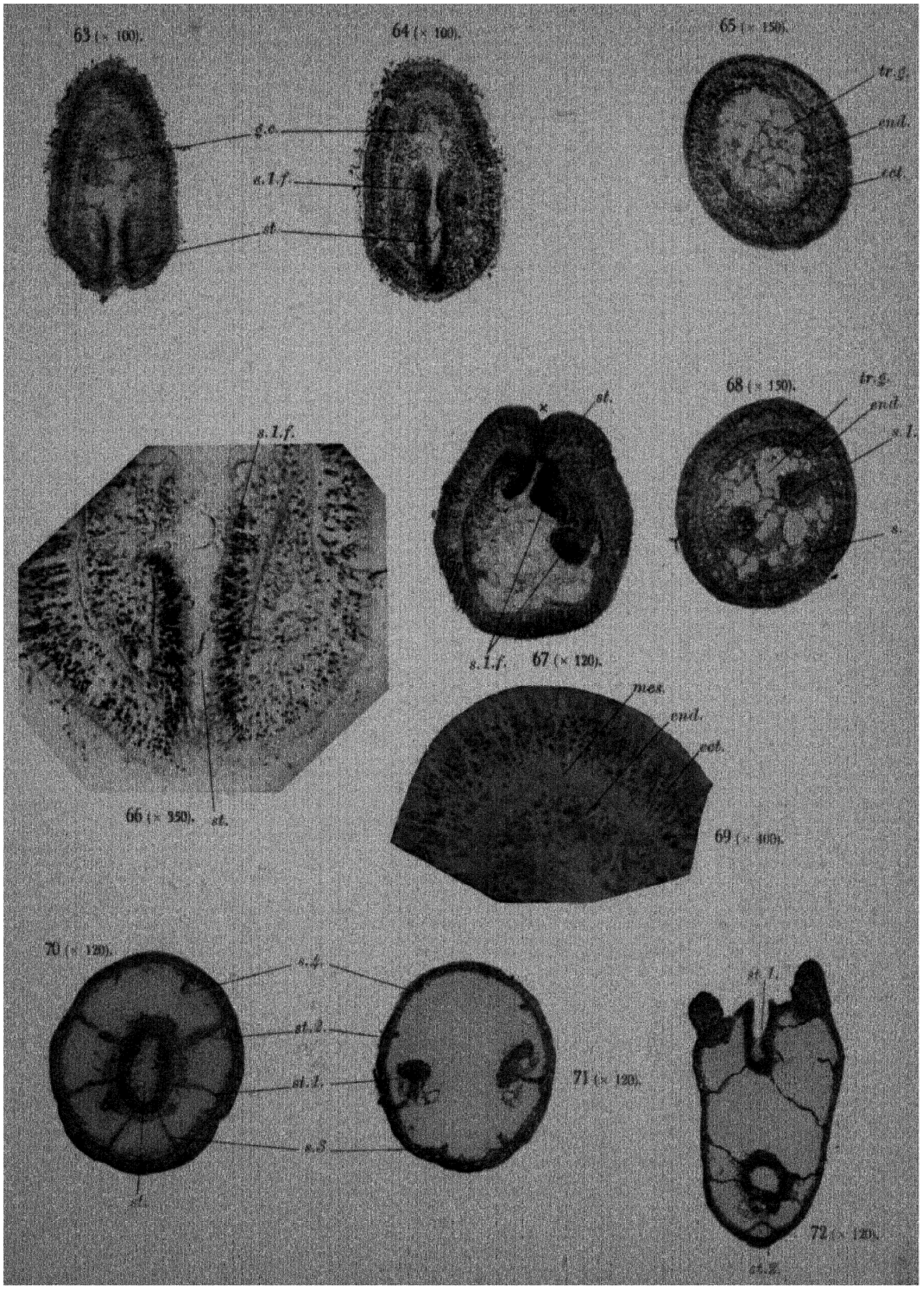

63 (× 100).
g.c.
s.l.f.
st.
64 (× 100).
65 (× 150).
tr.g.
end.
ect.
68 (× 150).
tr.g.
end.
st.
s.l.f.
67 (× 120).
mes.
end.
ect.
69 (× 400).
66 (× 350).
st.
70 (× 120).
s.g.
st.2
st.1.
s.8
st.
71 (× 120).
st.1.
72 (× 120).
st.g.

Fig. 71.—Transverse section through middle of gastric cavity in same specimen as last. The sulco-lateral mesenteries are the only ones which have as yet received a "mesenteric filament" border.

Fig. 72.—Section through a young double-monster anemone of same age as that shown in last figure. The section passes obliquely through the mouth of one of the heads and transversely through the stomodæum of the other. The base was single. Corresponding mesenteries came together and became fused at the region of transition from the double to the single condition.

# X.—*The Morphology and Evolution of the Ambulacrum in the Echinoidea* Holectypoida.

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## Introduction.

During the course of the work upon which the following pages are primarily based, the need for an ever-increasing width of scope has continually arisen. In its original conception the paper was to treat of the structure of the *Holectypoida* alone. Gradually the inevitable comparisons extended their range, until in its final form the work deals more or less completely with the ambulacral structure of all the orders of the Echinoidea, and includes far more argument of a general type than was first intended. Nevertheless, the original title has been retained. As in a map designed to show the position of a town, a large area of the surrounding district must needs be included, so that the roads which lead to, from, or past the place can be distinguished; thus, too, the relative position of the Holectypoid ambulacrum in the morphogenesis of Echinoid ambulacra can only be appreciated by description of the homologous structures which preceded, succeeded, or diverged from it in the course of evolution. Thus the title, though far from comprehending all the matter subjoined to it, is apt, in that it indicates the central topic towards which all the others converge and contribute.

In the study of the Echinoidea, the ambulacra and their associated structures have always been recognised as affording taxonomic evidence of great value. Not only do the "avenues" of pores attract attention, in denuded tests, by their distinctness and diversity, but the extensions of the water-vascular system to which they give passage are concerned with many vital functions. Ambulacral plates are among the first to appear during the metamorphosis of an Echinoid pluteus, and the development of ambulacral projections from the hydrocœl marks an early stage in larval life. An ambulacrum consists of an even number of columns of plates (usually two), each one of which is perforated for the transmission of a "tube-foot." There are thus two features, more or less interdependent, that are available for study in fossil forms– the plates and the pores. But it is only within the last five decades that any consistent attempts at an understanding of the plating-structure of the Echinoid corona have been made; and even now systematic writers most frequently limit their descriptions of the ambulacra to the nature of the pores and the distribution of the ornament.

The tracing of sutures in the ambulacra of fossil Echinoids is usually attended with some difficulty, and is always in large measure dependent upon the preservation of the material. There are, however, few cases where no trace of ambulacral structure can be detected, and even in them the application of any granular stain, with or without etching, will often resolve the sutures. By the use of a mixture of alcohol and glycerine, recent forms may be made to yield the secret of their plate arrangement without retaining any permanent traces of the reagent. As a last resource, stereo-sections viewed in polarised light between crossed nicols will almost always show the outlines of the several plates by reason of the varied orientation of the calcite.

LOVÉN and DUNCAN were the pioneers in "osteological" investigation of Echinoid tests. The majority of the figures in the "Études sur les Échinoidees" (LOVÉN, 1875) are detailed analyses of coronal structure in a great diversity of forms, both recent and fossil. The "Revision of the Genera and Great Groups of the Echinoidea" (DUNCAN, 1889) was based mainly upon previous studies of ambulacral structure made by its author. The works of these two writers gave a great impetus to truly morphological study of the Echinoidea; points of morphological importance are rarely emphasized in publications bearing a date earlier than 1875.

The present paper is divided into two parts. The former comprises a summarised account of the known characters of the ambulacra in the regular Echinoidea, followed by discussion of various aspects of ambulacral structure and the principles involved in its development. The concluding sections of this part consist of a comparison between the functions and structures found in regular and irregular Echinoids, and so serve as a statement of the evolutional problems whose solution is likely to be found in the annectant order of the *Holectypoida*. The second part is concerned chiefly with detailed description of the ambulacra of representative species of that order, after which follows an attempt to ascertain the course of ambulacral evolution which is thereby indicated.

There remains the seemly and pleasant duty of recording the names of those fellow-workers who have given help in the completion of this study. Those Echinologists, dead and living, who have unwittingly contributed towards the work by their writings, are mentioned throughout the text, and recorded in the list of literature at its close. Much of the morphological work has necessarily been done upon material in the writer's collection, since the investigations often resulted in the destruction or mutilation of the specimens. Most of those that have survived are now in the palæontological collection of University College, Reading. But among those geologists and palæontologists who have willingly afforded opportunity for the examination of their private collections, or of those entrusted to their charge, especial mention must be made of Messrs. G. E. DIBLEY, J. W. JACKSON, L. RICHARDSON, Prof. W. J. SOLLAS, Messrs. LL. TREACHER, T. H. WITHERS, and G. W. YOUNG. To Dr. F. A. BATHER, Dr. H. L. CLARK, Mr. J. COTTREAU, Prof. L. DOLLO, Dr. R. T. JACKSON, Mr. J. LAMBERT, Dr. G. STEFANINI, Mr. P. THIÉRY and DOM A. VALETTE gratitude is due for the gift or loan of copies of their own and other publications to which access would otherwise have been difficult or intermittent. My thanks are extended to Dr. G. HICKLING and Mr. D. M. S. WATSON for their ever-patient attention to sometimes wearisome expositions of my views, and for the stimulus of their frank and fraternal criticism. Lastly, for that critical and sympathetic encouragement that is so necessary for one whose work is carried on in relative isolation, I rejoice to place on record my indebtedness to Drs. F. A. BATHER, R. T. JACKSON and H. WOODWARD. Particularly during the time when most of the manuscript was written, when mental depression was almost inevitable owing to the

chaotic state of the world, the stimulating approval of these masters of research was especially helpful.

## PART I.—(1) The Evolution of Ambulacral Structure in the Regular Echinoidea.

### (a) *Preliminary Note.*

In this section a summary is given of the general characters of ambulacral structure in the corona of the Regular Echinoidea. The account is only to a small degree original, and to a less extent exhaustive. It is necessary, however, to prefix a *résumé* of this kind to the morphological and morphogenetic considerations of the succeeding sections. Although but few of the observations recorded are new, it is believed that the facts already known are here first collected into a coherent scheme, and that they are interpreted in a fresh manner.

For the ambulacral characters of the Palæozoic Echinoids, I have relied almost entirely on Jackson's "Phylogeny of the Echini" (1912). The account of these structures in the other Regular orders has been gathered from a very large number of sources.

The classification adopted for the post-Palæozoic forms is that given by Gregory (1900). Although the more recent taxonomic system of Jackson (1912) is available, and in some respects preferable, it has proved more satisfactory to treat of the morphology of the ambulacra in association with the older scheme. This is doubtless due to the close accord between Gregory's classification and that of Duncan (1889); the latter was based mainly on ambulacral characters. The section was originally written out on Jackson's system, but the result abounded in repetition and failed to bring out the morphogenetic facts clearly. Whether this was due to defects in the classification, or to the existence of numerous lines of parallel development, is a matter that cannot profitably be considered here. Systematic discussion is out of place in a paper devoted to purely morphological topics; especially since reference to non-Holectypoid orders is merely incidental to the main purpose of the work.

### (b) *Bothriocidaris.*

Bothriocidaris is not merely the oldest Echinoid known but morphologically it approximates remarkably to the theoretical phylembryo of the class. It is necessary, therefore, that the ambulacral characters of this interesting form should be understood, before their subsequent modifications can be co-ordinated. Thanks largely to the work of Jackson, such knowledge is now available. The descriptions and figures given by him (1912, pp. 53 and 240, Plate 1), supply the evidence upon which the following summary is based.

The ambulacral areas are each built of two columns, composed of a few high hexagonal plates which alternate in position with one another, and with those of

the contiguous interambulacral columns. It is hardly too sweeping an assertion to make that, save for the presence of podial pores in the ambulacrals, the corona is practically undifferentiated into ambulacral and interambulacral areas. Belief in the archaic quality of the Bothriocidaroid ambulacrum is supported (as has been shown by JACKSON, LOVÉN, and others) by the early ontogenetic phases of the ambulacra of many diverse types of Echinoids. The post-larval *Goniocidaris canaliculata* so exquisitely figured by LOVÉN (1892, Plate 2, here adapted, Plate 61, fig. 2), may be regarded as typical of this line of evidence. Further, as JACKSON has remarked (1912, p. 60), those ambulacral plates of advanced Spatangoids which have become obsolescent owing to loss of function by their podia, tend to revert to proportions and relations to the interambulacrals, strikingly similar to those found in Bothriocidaris.

In Plate 61, figs. 2–6, a series of ambulacra showing "Bothriocidaroid" characters is given. All the figures are brought to the same size, regardless of the actual dimensions of their originals. Figs. 2, 3, and 4 illustrate early ontogenetic phases in species representing the diverse orders of Cidaroida, Clypeastroida and Spatangoida. In the case of Goniocidaris and the adapical region in Mellita, the adult ambulacrals are utterly different in proportions from the neanic plates. In Brissopsis this difference is not so marked, owing to the (probably) regressive character of Spatangid ambulacra. This quality is clearly indicated by the two adult ambulacra of Spatangid genera shown in figs. 5 and 6. In all these figures it will be noted that "Bothriocidaroid" characters are indicated, not merely by the shape of the ambulacrals, or the disposition of the pore-pairs, but to a large degree by the alternation of the ambulacral and interambulacral plates. Such a series, which might be very greatly extended, seems to establish the fundamental nature of the Bothriocidaroid ambulacrum so firmly that it may be considered proved in default of contrary evidence.

For the purpose of the present paper it is unnecessary to enter into a discussion as to the origin and homologies of the Echinoid ambulacrum as such. Whether the ambulacral plates are modified from some Diploporitan Cystid ancestor, or are homologous with any parts of Asteroid or Blastoid ambulacra, matters little in a description of so advanced a structure as the Holectypoid corona. It is sufficient to accept the Bothriocidaroid ambulacrum as a "fait accompli," and to start from that as a basis. It seems, therefore, safe to assume that the primitive ambulacrum, from which all other Echinoid ambulacra were derived, possessed the following essential qualities :—

(i) Each area consisted of two columns of similar plates.

(ii) Each plate was hexagonal in shape, and at least as high as broad.

(iii) The number of plates in each column was no greater than that in the interambulacral columns.

(iv) The pore-pair was situated centrally in each plate, and the pores of a pair were superposed, the line of podial perforations thus being practically straight from the apex to the peristome.

### (c) *The Palæozoic Echinoidea.*

The earliest available evidence for an enquiry into the subsequent modification of Bothriocidaroid structures is found in the Upper Silurian. During the intervening period of Echinoid evolution at present unrepresented, two changes of far-reaching importance were initiated in the ambulacra. The four genera known from the Silurian are Palæechinus (Plate 61, fig. 7). Koninckocidaris, and the rather anomalous Palæodiscus and Echinocystites. With the exception of the last-named, these genera have ambulacra of closely similar types. The areas are very much narrower in proportion to the interambulacra than in Bothriocidaris, and the individual plates are low and lath-like in form. The areas are straight, so that the perforations for the podia constitute long lines of mechanical weakness, aggravated by their great numbers and close approximation. Owing to the reduced height of the plates, the number present in each column is enormously increased, and at the same time alternate interlocking with the still large interambulacral plates is impossible. So far from the maintenance of such rigid stability of the test, the interambulacral plates were able to slide across the ambulacra along the adradial sutures, in conformity with the general coronal flexibility.

Such long straight zones of weakness in the corona clearly required considerable modification if their owners were to survive. Granting the need for a greater number of podia than could be accommodated in the Bothriocidaroid ambulacrum, a remedy which inevitably produced great mechanical disadvantages was of doubtful merit. The ambulacrum of Palæodiscus, and to a less degree that of Palæechinus and Koninckocidaris, contained a very large proportion of "sutural tissue" as compared with stereom; and the plates themselves were drilled by the podial pores in a continuous line comparable with the perforation of a sheet of postage stamps with a corresponding liability to rupture.

Even at this early stage of Echinoid evolution, an attempt to circumvent the weakening effect above indicated is to be found in the ambulacrum of Echinocystites. The ambulacral plates in this genus are arranged in four columns; so that, for a given number of pores, the height of each plate is doubled in comparison with Palæodiscus. Moreover, the podial perforations are thereby arranged in more distant series. The phase of ambulacral development reached by Echinocystites was almost exactly repeated in lower carboniferous times by Lovenechinus (Plate 61, figs. 10, 11, and 13); and it is closely copied by *Echinocardium cordatum* (Plate 69, figs. 4 and 5) at the present day. It may be regarded either as a special type of "plate-crushing," with the production of alternate demi- and occluded-plates, and the complete suppression of primaries, or as the first stage in the development of "klasma-plates." Whether there is any real distinction to be maintained between the two alternatives is doubtful.

There are three Echinoid genera that arose in the Devonian: Lepidocentrus,

Pholidocidaris, and Lepidesthes. These three types represent very clearly two distinct morphogenetic trends as regards the ambulacra. In Lepidocentrus, the simple, narrow ambulacra are constructed on practically the same lines as those of the three Silurian genera first considered The plates of each column are all primaries, and are reduced to very slender proportions. All the disadvantages attached to the "Palæechinoid" ambulacrum are here maintained and even increased. The other genera, Pholidocidaris and Lepidesthes (Plate 61, fig. 12), mark a great and irretrievable advance along the lines of modification first shown in Echinocystites. At least six columns of plates occur in each area in Pholidocidaris, and eight in Devonian species of Lepidesthes; and the areas themselves show a considerable increase in proportionate width.

During the Carboniferous and Permian periods, the style of ambulacral structure, initiated by Echinocystites and elaborated by Pholidocidaris and Lepidesthes, was maintained and amplified in such forms as *Lepidesthes extremus*, with sixteen columns, Melonechinus (several specimens) with twelve, and *Meekechinus elegans* with twenty, in an area. This multiplication of ambulacral columns (harmonising with similar developments in the interambulacra) resulted in the widening of the areas back to and beyond their proportions in Bothriocidaris, and at the same time gave passage to enormous numbers of podia. In any but flexible tests, such a multiplicity of sutures and perforations would have involved impracticable fragility; and with the on-coming of rigidity in Permo-Triassic times, this highly specialised character completely disappeared. The ambulacra of Meekechinus afford a striking illustration of the often fatal exuberance of evolutional activity associated with races of animals in the early stages of their existence.

The majority of post-Devonian "Perischoechinoida" adopted or maintained the more static type of ambulacral structure shown in Lepidocentrus. Hyattechinus (Plate 61, fig. 8), in spite of the peculiar specialisation of its podial pores, has uniformly simple ambulacral plates. Most of the genera, however, show signs of an endeavour to counteract the weakening effect of a narrow, much-sutured ambulacrum, although the attempts are more moderate than those shown by Echinocystites. In some genera, such as Lepidocidaris (Plate 61, figs. 15 and 16), Maccoya (Plate 61 fig. 9), Lepidechinus and Perischodomus, premature efforts at "plate-crushing" are seen, similar in many respects to that developed in so many of the Euechinoidea, particularly in the phyllodes of the "Cassiduloida." The plates tend to become cuneiform rather than lath-shaped, and some are excluded altogether from the adradial or perradial lines, and in rare cases from both. All these early, halting experiments in the direction precipitately taken by Lepidesthes seem to have met with the fate normal to precocity, and did not endure beyond the Palæozoic era. They are morphologically interesting, as illustrating the failure of a structural tendency which, revived with certain modifications, proved eminently efficient and successful at a later date.

In this connection the relation between "klasma-plates" and the products of "crushing" in Euechinoid ambulacra may be considered. The essential distinction between the scaly, multiporous ambulacra of such a form as Melonechinus, and the equally complex adoral parts of the areas of Heterocentrotus (see Plate 64), consists in the greater development of occluded plates, and the absence of true combination in the former. It seems reasonable to suppose that the ambulacra of Echinocystites, Maccoya (Plate 61, fig. 9), and Lovenechinus are morphogenetically ancestral to the complicated areas of Melonechinus and Lepidesthes. In the case of Lovenechinus (Plate 61, figs. 10 and 11), the young plates are ontogenetically and morphogenetically simple, and gradually attain some degree of occlusion during growth. An acceleration from the mid-zonal characters of Lovenechinus would lead inevitably in the direction of the formation of "klasma-plates." Thus it may be presumed that the apparently distinct columns of such plates that occur in the Melonechinus series were derived by over-development of the more restrained complication shown in the simpler types.

In passing, it may be remarked that the ambulacrum of Lovenechinus, in its highest state of development, is almost identical in structure with the petaloid part of Area III in *Echinocardium cordatum*. A comparison of Plate 61, figs. 10 and 11, with Plate 69, fig. 5, will make this resemblance clear. A point of morphogenesis of extreme interest is thereby indicated. *E. cordatum* is one of the most highly specialised, as it is one of the latest, of the Spatangidæ, which, for reasons indicated in Section 2 (c) below, has had occasion to develop secondary ambulacral complexity. It has carried out this development along strictly "Perischoechinoid" lines. Hence, if *E. cordatum* be regarded as phylogerontic (a reasonable hypothesis), the recrudescence of phylobrephic structure seems to imply that reversionary tendency in racial old-age that has been aptly termed "second-childhood." In a recent paper, L. F. Spath (1919) draws attention to the fact that the suture of *Indoceras baluchistanense*, Noetling, with 37 lobes and 38 saddles, recalls the "acme of specialisation among Triassic Ammonites." He argues that this, one of the last of the Ammonites, fails to reveal gerontic characters, and ascribes the sutural elaboration to environmental conditions. By a similar argument, Lovenechinus should have been a burrower in the sand like Echinocardium, but such a supposition appears grotesque, in view of its general structure. May not Indoceras afford another illustration of imperfect atavism in a gerontic form?

In certain Carboniferous genera, of which Archæocidaris (Plate 61, fig. 14) may be considered typical, an entirely different modification appears. The individual ambulacral plates retain the simple "Palæodiscoid" arrangement and proportions, while the whole area becomes sinuous in its course. This quality has an advantage over the other experiments in that, while the number of plates may be very considerable, the much-sutured areas (and the much-perforated pore-fields) no longer constitute straight cleavage lines in the corona. So long as the ambulacra were composed of widely-sutured plates, and were devoid of the superficial cementing

influence of large tubercles transgressing the sutures, the quality developed in Archæocidaris represents the best obtainable result, at least as regards the mechanical strength of the test.

In respect of its ambulacral structure, Archæocidaris bears a relation to post-Palæozoic Echinoids similar to that borne by Bothriocidaris to the class as a whole. The earliest Euechinoids (the Cidaroida) all possessed narrow, sinuous "Archæocidaroid" ambulacra, and the morphogenetically young plates of these areas in practically all Regular Euechinoids are simple, lath-like primaries.

### (d) *The Cidaroida.*

The Permo-Triassic epoch, during which so many changes of a fundamental character occurred in the evolution of most groups of animals, saw the extinction of all forms of Echinoidea other than those with "Archæocidaroid" ambulacra. At the same time, with the stereotyping of the "Euechinoid" pattern, the corona progressively lost its flexible nature, becoming almost perfectly rigid by Liassic times. A detailed and interesting account of this change is given by Bather (1909, pp. 250–256). Relative rigidity of the test-fabric constitutes almost the only important difference between Cidaris (*sens. lat.*) and Archæocidaris. In the ambulacra the condition of sinuous, narrow areas built wholly of primaries, introduced in the Carboniferous genus, was maintained with scarcely any modification in the early Cidaridæ; and, save for a lack of imbrication and the presence of increased granular ornament, persists unchanged in the living members of the group.

The plating of the ambulacra, although always primary, is not in every case regular. In *Paracidaris florigemma* (Plate 62, fig. 1) and several other Cidaridæ with strongly sinuous areas, strict alternation of the columns is interrupted where the curve is sharp. An additional plate is incorporated into the column with convex curvature. This does not imply dissimilarity in the number of plates in the two columns of an area, since such supernumerary plates occur in each column alternately. Such a development is obviously a mere adaptation to the shape of the area, but its appearance suggests a problem and a comparison.

If the usually accepted view of the growth of the Cidaroid ambulacrum is correct, the ambulacral plates pass in a gradual stream from the apex to the peristome, where their advancing front is resorbed, the whole process suggesting comparison with the movement and fate of a glacier. The interambulacra perhaps undergo a similar movement, but not at the same velocity. Such a streaming of the columns would mean that any individual ambulacral plate would at some time occupy a position at the convex curve of its column, and subsequently descend to a straighter region, eventually reaching the concave curve. Since the plates in the convex portion are specially modified (in some species) to fit their surroundings, and similar plates never occur in other parts of the columns, it is clear that a very great amount of resorption and sutural readjustment would be necessary if the streaming actually occurs.

Probably the production of the extra plates does not begin until relatively late in ontogeny; it has been detected only in adapical parts of the ambulacra, where the curvature is most marked.

Reference to Plate 62, fig. 3 (Salenia), will show that in the small and retarded group there illustrated, the entire ambulacrum (excepting the morphoneanic region) may be composed of plates alternately related to one another exactly like those at the corners of the Cidaroid ambulacrum. In spite of the gently curved course of the Saleniid areas, there is no special connection between the plating and the curvature; but it is a point of some importance that a quality occurring locally (probably as a morphogerontic feature) in some Cidaridæ is regional and persistent in the Saleniidæ. Again, in *Hemicidaris intermedia* (Plate 62, fig. 14), the ambulacrals situated between the adapical primaries and the triple compounds tend to group themselves into a Saleniid pattern. This is most regular in the left-hand column of the specimen figured; there it is plainly associated with the formation of "dyad" compounds.

In the Diplocidaridæ (Plate 62, fig. 2), two interesting modifications of the normal Cidaroid structures appear. The pore-pairs are biserially arranged, probably under the influence of the same mechanical necessity that produced complexity in the Palæozoic Echinoidea. It may be remarked in this connection that this family includes species whose average dimensions are considerably greater than those of the Cidaridæ: this may well be connected with the reduction of fragility achieved by the displacement of the podial pores. The plates are alternate in character in correspondence with the pore-pairs. Those plates which have adradiad pores are relatively high (particularly in the perradial tract), and support granules that are practically secondary tubercles. The plates with perradiad pores are low, and support very minute granules only. In the case figured by DE LORIOL, and here copied, there is reason to believe that the perradial suture is incorrectly represented. I have been unable to examine species of Diplocidaris in which sutures could be detected, but it seems inevitable that the relations of the plates of the columns should be similar to those of Salenia. In any case, the plates of Diplocidaris are grouped into potential dyads, although there is no true combination. The Diplocidarid ambulacrum thus bridges the morphogenetic gulf between the Cidaroida and such simple Diademoida as the Saleniidæ and the Triassic (?) Diadematidæ described by BATHER (1909, p. 254).

The usually dissociated condition in which fossil Cidaridæ are found, and the ready collapse of dried recent specimens, show that the ambulacra produce serious lines of weakness in the test, in spite of their sinuous course. As is shown in Section 2 (e) below, Cidaris has but feeble powers of adhesion by means of its podia, relying more on its long radioles for protection and entanglement. No advance which involved exposure to rough treatment by waves or adversaries was possible for an organism endowed with so mechanically unsound a fabric.

In ambulacral structure, as in most other morphological features, the Cidaridæ have maintained that conservatism of type that characterises the root-stocks of most

classes of animals; and this fact alone is sufficient reason for the reference of all more elaborate developments back to the Cidaroid ambulacrum as a starting-point.

### (e) *The Diademoida.**

The non-Cidaroid Euechinoidea Regularia comprise a large and varied series of forms which have been, on the whole, markedly progressive in evolution from their inception in Triassic times to the present day. While differing from the Cidaroida by many obvious characters, the Diademoida show a steadily increasing contrast in their ambulacral structure. The areas become wider than in Cidaris, lose their sinuous character, and come to support tubercles equal in size to those of the interambulacra. Moreover, a considerable increase in the number of podia in a column (and thus inevitably of plates) is achieved; and hence the mechanical difficulties incumbent upon the Palæozoic Echinoidea demand solution anew. The displacement of the pore-pairs from a uniserial course is essential if any strain is to be applied to the test in their neighbourhood, and the more advanced Diademoida can exert the function of podial adhesion to a remarkable degree. This necessity for the multiserial arrangement of the pores involves corresponding displacement or irregular development of the plates. But instead of producing a multicolumnar area like that of Lepidesthes, the reaction of the Diademoid type has resulted in a far higher degree of strength than that attained by the Cidaroida. The plates become massed together into varying groups; the amount of sutural tissue between the components of a group is much reduced; and the welded plates are bound together by the extension over their outer surfaces of the closely-knit stereom of one or more large tubercles. The compound plates thus formed function mechanically as simple, high, multiporous plates of more than Bothriocidaroid strength and proportions, often alternating regularly with the contiguous interambulacrals after the manner of those of the Ordovician prototype.

(i) *The Calycina.*—This group of Echinoids was one of the earliest of the Diademoida to appear, and has retained very constant characters up to the present day. Possibly represented in the Trias (see Bather, 1909, p. 100), it is one of the best known sub-orders in the scanty Echinoid fauna of the Lias. Due probably to the generally small size of the species, the group is morphogenetically much retarded in practically all respects, and in none more than in the ambulacra. The Acrosaleniidæ, although the earlier family to appear, comprise rather larger forms than the Saleniidæ, and are somewhat more advanced in ambulacral structure. It will, therefore, be simpler to consider the latter family at the outset, since its characters, though due to phyletic retardation or regression, are the more primitive from the standpoint of morphology.

Salenia (Plate 62, fig. 3) has narrow, sinuous ambulacra which rarely support

* I retain the old-established name for this order and its sub-divisions to avoid confusion, since Gregory's classification is here adopted. This does not imply disbelief in the rational and legal superiority of Jackson's term, "Centrechinoida."

ornament of a larger type than granules, although a few small tubercles may occur near the peristome. The morphoneanic plates near the apex are simple primaries for a short distance, though they resemble the plates of Diplocidaris in that they are alternately largely and minutely granulate. From a point not far from the ocular plate to the peristome margin, these plates become grouped into dyads by the perradial reduction of the minutely granulate ambulacrals, but there are rarely any demi-plates present, and true combination is restricted to the adoral parts of the areas. I have never seen any triads in the various species of Salenia and Peltastes that I have examined, so that the few compound plates that exist in the family seem to be of the simplest possible type. Such a condition is comparable with that found in "Diadematoid ambulacrum *a*" from the Trias of BAKONY figured by BATHER (1909, Plate 69, fig. 215), and so may be considered to be truly primitive. Whether the simplicity in the case of the Saleniidæ is due to retardation or actual regression is uncertain; a further discussion of the question will be found in Section 2 (f), below.

Acrosalenia (Plate 62, fig. 4) shows a considerably more advanced type of structure than Salenia, although the ambulacra are still far from complex. In spite of minor specific differences, all of the lower Oolitic forms that I have examined have essentially the same qualities. The ambulacra of Acrosalenia have been described by various writers, a summary of whose views is given by THIÉRY (1911, pp. 4—6). That author gives drawings of four species (*A. spinosa*, *A. lycetti*, *A. lamarcki*, and *A. patella*), showing clearly, though somewhat crudely, the type of structure which, according to my experience, is universal in Lower Oolitic forms. (In Corallian types, according to DE LORIOL (1890), a greater development of triads and demi-plates occurs than in Bathonian species.) Adapically there is a considerable sequence of simple primaries in straight columns, the number of such plates varying with the species and perhaps with individual age. The granulation of the apicad plates is somewhat irregular, but on the whole the largest ornament is found on every third plate. Adorally to these primaries the plates become grouped into dyads, each pair separated by a normal solitary primary. Below the ambitus triads of the "Diademoid" type appear, the intervening primaries having become intimately associated with the pairs adapical to them. Demi-plates are rare, but each triad is very nearly "Arbacioid" in character, the median component being much expanded perradially. Although the plates are grouped almost throughout the area in some species, I believe that there is never any real combination except on the adoral surface.

(ii) *The Diademina.**—This sub-order contains the families Orthopsidæ, Diadematidæ, Pedinidæ, Diplopodiidæ, Phymosomatidæ and Echinothuriidæ. The Orthopsidæ, as their name implies, have ambulacra of extreme simplicity. The family as defined by Gregory ranges from the Lias to the present day; the modern representative, Aspidodiadema, being a deep water, probably regressive, type. The

* This and the following sub-order are considered in inverse sequence to that adopted by GREGORY. Morphologically and chronologically the Diademina are earlier than the Arbacina.

ambulacral plates are all primaries, and alternate regularly along the perradial suture. The ornament, however, is more elaborate than that of the Cidaroida, and shows that the plates are grouped in a manner corresponding with that of the simpler parts of the Acrosaleniid ambulacrum. In Orthopsis (Plate 62, fig. 5) fairly large secondary tubercles occur on every third ambulacral, and are so situated that they extend almost equally over two contiguous plates whose dividing suture passes under the mamelon. These two plates are more or less thoroughly combined into dyads, and between each pair intervenes a solitary primary which is not combined. This condition, as the ambulacrum of *Acrosalenia* shows, is preliminary to the development of triads. The Orthopsidæ thus resemble the Calycina in the stage of ambulacral development attained; and like that group, have been persistent in range and conservative in structure.

The Diadematidæ and Pedinidæ (which are united by JACKSON under the name of Centrechinidæ) show the typical "Diademoid" type of ambulacral plating, although many genera possess somewhat greater complexity in parts of the areas. There is always a considerable number of primaries in the adapical parts of the ambulacra, and these are normally tuberculate on every third plate in preparation for subsequent combination. Towards the peristome the adoral member of a triad is liable to become separated from the perradial suture, thus producing a partially "Arbacioid" result. It is, however, very rare to find a true "Arbacioid" plate, though such do occur sporadically. In many Oolitic and Cretaceous genera, such as "Plesiodiadema" and "Placodiadema," the compound plates at the mid-zone or above it are occasionally built of four, five, or even more, components. Usually, all the combined plates are primaries, but in a few cases one or more of them may be demi-plates. The recent forms are normally "Diademoid." The irregularity of the compounds in the Upper Jurassic and Lower Cretaceous genera is particularly interesting, since it was during that time that the family Phymosomatidæ probably arose from a Diademoid stock. As that family has persistently complex compounds, the occurrence of similar developments in numerous Diadematid genera seems to imply the existence of morphogenetic plasticity throughout the group, preparatory to the specialisation of a new type.

Among the Pedinidæ, Stomechinus and Astropyga show points of considerable morphological interest in the structure of their ambulacra; while Noetlingia, if the genus is rightly to be included in this family, presents an unique type of specialisation. In Stomechinus (Plate 62, fig. 7) normal "Diademoid" triads are the chief ingredients of the areas, but they are often ill-defined. "Arbacioid" compounds are practically never found. But the tuberculation of the ambulacra is somewhat sporadic, except in the adoral parts, with a tendency to repetition on every sixth plate rather than on every third. This feature gives a result that could readily be transformed into the condition found in Astropyga. It is a matter of much difficulty to determine the degree of combination attained in Stomechinus, but, after the examination of many

naturally and artificially "weathered" specimens, I incline to the opinion that the plates are merely grouped on the adapical surface, and do not enter into true combination until the ambitus is reached. Astropyga (Plate 62, figs. 8 and 9) has normal "Diademoid" triads adapically and adorally, but in the mid-zone (which extends for some distance in both directions from the ambitus) these triads are definitely united in pairs to produce hexads, or "super-compounds." This tendency, which is found in such diverse genera as Acrocidaris, Stomopneustes, Echinus, Tripneustes, and probably Heterocentrotus, seems to mark the furthest stage in ambulacral combination that is reached by any Echinoid. Astropyga represents the culmination of "Diademoid" structure. Discussion of the aberrant genus Noetlingia, which LAMBERT (1906) associates with Stomechinus, is deferred to the purely morphological arguments in Section 2 (d). It is sufficient here to note that the greater part of each ambulacrum consists of dyads with intervening occluded, uncombined plates, in which the pore-pairs are obsolescent. Adorally, the ambulacra are comparable with the simple parts of those of Acrosalenia, having dyads separated by simple primaries.

The Diplopodiidæ (Plate 62, fig. 6) have the peculiar quality (shared with the Phymosomatidæ) of biserial pore-pairs adapically; but, apart from the inevitable irregularity of the transverse sutures of the plates in that region, they do not seriously differ from the Oolitic and Cretaceous Diadematidæ. In one further respect, however, Diplopodia shows a distinct bias in the direction of Phymosoma. The compound plates are usually tetrads or pentads in the mid-zone, and the extra component or components are normally demi-plates intercalated between three normal "Diademoid" primaries. The plates in the biserial parts of the areas are more or less clearly grouped into triad, tetrad, or pentad series, but rarely, if ever, show signs of being truly combined.

The Phymosomatidæ (Plate 62, fig. 13) show many interesting ambulacral features. The adapical pore-pairs are usually biserial (though to a less extent than in Diplopodia), and the compound plates of the mid-zone are normally pentads built of three "Diademoid" primaries with two contiguous intercalated demi-plates. The compounds near the peristome are tetrads hardly distinguishable from those at the mid-zone of Diplopodia. Perhaps the actually proximal plates may be triads. There can be little doubt that, morphologically, the Phymosomid ambulacrum was derived by the amplification of an area constructed on the Diplopodiid pattern. It is a point of importance to note that, in spite of the greater complexity of the compounds in Phymosoma, the actual number of ambulacral plates in each column is very considerably less than in Diplopodia or Stomechinus. Clearly, simple "plate-crushing" cannot have been the chief factor in the determination of the structure. The course of the sutures within the compounds is instructive. They all tend to converge to the mamelon of the tubercle, while the perradial ends of the demi-plates are usually buried beneath it. The sutures of the primary constituents

are very suggestive of those of the Arbaciidæ, especially below the mid-zone. However, the plates always reach the perradial suture. Lastly, the Phymosomid pentads alternate very regularly with the contiguous interambulacrals, so that the compound plates have attained proportions and relations which recall those of the simple plates of Bothriocidaris.

The anomalous group of the Echinothuriidæ, which arose in the Corallian with Pelanechinus, and is represented by several living genera, is probably reversionary in character. The imbrication of the coronal plates invites comparison with the Palæozoic Echinoidea, but it is hardly possible that any direct phyletic connection can unite the two series. The ambulacra are composed of dissociated triads for the greater part of their length. Towards the peristome the reduced ambulacrals assume a remarkable resemblance to "klasma-plates," although their disposition is altogether unlike that in the Palæozoic forms. In both groups the parallelism of ambulacral structure may safely be ascribed to adaptation for coronal flexibility.

(iii) *The Arbacina.*—This sub-order contains the two families Hemicidaridæ and Arbaciidæ, which may be roughly defined as Mesozoic and Cainozoic groups respectively. In Hemicidaris (Plate 62, fig. 14) the adapical parts of the ambulacra are truly Cidaroid in character, being narrow, sinuous, almost devoid of tubercles, and built wholly of primaries. JACKSON considers this to be a regressive quality, but, for reasons given in Section 2 (f), I incline to consider it truly primitive, although perhaps retarded. About midway between the apex and the peristome the plates begin to be associated into groups of two or three, the middle one (in the latter case) bearing a tubercle. Gradually, as the area is traced adorally, these triads become welded together into true compounds, and often one (rarely both) of the outer components becomes squeezed out from the perradial suture. When demi-plates occur, the compound takes on the "Arbacioid" character recognised by DUNCAN, the central, tuberculate member of the triad retaining its primary nature. In those triads which support the less prominent tubercles, the structure of the compounds is typically "Diademoid." DUNCAN (1885, *b*) has figured a case of the production of a tetrad in *H. intermedia*, but my experience shows this to be an exceptional, and probably accidental, quality. In the case that DUNCAN illustrated, the adapically succeeding compound is a dyad; so that, as he recognised, the adoral member of this compound has become attached to the wrong group. Such an abnormality is of interest, as showing a possible way by which polysynthetic compound plates may have originated. A somewhat analogous case is shown in the two lowest compounds in fig. 14. It is noteworthy that in Hemicidaris the pore-pairs tend to be arranged in an arcuate plan on each compound plate. Figures and descriptions of the ambulacral structure of many species of Hemicidaris are given by DE LORIOL (1890). In one form, *H. mondegoensis* (here Plate 62, fig. 12), the compounds of the mid-zone are double, and they are Diademoid in character, corresponding with those of Astropyga. In *H. valleti* (DE LORIOL, 1890, Plate 14, fig. 2, *b*) a type of "Arbacioid"

structure closely similar to that of Tetrapygus occurs. The mainly "Diademoid" triads of Acrocidaris (Plate 62, fig. 11) seem usually to be grouped into super-compounds at the mid-zone. The ambulacrum of *Glypticus hieroglyphicus* (Plate 62, fig. 15), according to LAMBERT and THIÉRY (1908, p. 24), shows an unusual type of triad formation. Each compound plate is built of an adapical demi-plate, a median primary that is almost a demi-plate, and a perradially expanded adoral primary. Such a structure suggests the development of dyads made of unequal primaries (the presumed primitive type of compound plates), which almost crowd out the intervening solitary plates before they unite with them. Codiopsis, according to DE LORIOL (1890), has similar ambulacra, and the structure of Noetlingia is possibly analogous.

The Arbaciidæ form a well-defined family of Tertiary date. In Cœlopleurus (which was studied in great detail by DUNCAN and SLADEN, 1885, *b*), the greater part of each ambulacrum is made up of triads of ideally "Arbacioid" type, *i.e.*, of a central primary and two demi-plates let into its adoral and adapical margins respectively. In Arbacia and Tetrapygus (Plate 63, fig. 1) a higher degree of complexity is reached. But few uncombined plates occur adapically. These are followed by typical "Arbacioid" triads alternating with individual plates which, whether primaries or not, are distinct from the compound plates. This condition is almost exactly paralleled in the ambulacrum of *Hemicidaris valleti*, de Loriol. At or near the ambitus these independent plates become incorporated into the triads adoral to them, thus producing tetrads; but over the greater part of the adoral surface the compounds are built fairly constantly of five elements. The "Arbacioid" plan is none the less evident, although the adoral demi-plate becomes disconnected from the adradial suture, and constitutes an "included plate." This most instructive type of ambulacral structure is further discussed in Section 2 (c), below. Leptarbacia (Plate 62, fig. 16), a Cretaceous genus recently introduced by CLARK and TWITCHELL (1915) has a superficially complex ambulacral plating that is probably similar in essentials to that of Tetrapygus. It is not possible to tell from the figures and descriptions available whether the small demi-plates are free or combined, but from a consideration of their sutural relations the former condition seems the more likely. It is equally uncertain whether this small Cretaceous form should be classed with the Arbaciidæ.

(iv) *The Echinina.*—This group of the Diademoida corresponds very nearly with the division Camarodonta proposed by JACKSON, the only genus differently placed by that author being the recent Stomopneustes. There are four families, of which the Temnopleuridæ arose in the Cretaceous period, while the Triplechinidæ, Strongylocentrotidæ, and Echinometridæ are of Cainozoic date. The two families first named show a remarkable constancy of ambulacral structure (see Plate 63, fig. 2). Triads of the "Echinoid" pattern (two primaries enclosing a demi-plate, or one primary with two unequal demi-plates adapical to it) build practically the entire

area from apex to peristome. A modification of this character is found in Tripneustes among the Triplechinidæ. Here, as DUNCAN and SLADEN showed (1885 *a*, Plate 5, fig. 4), in "*Hipponoë*" *proava*, from the Indian Miocene, the triads unite in pairs with such intimacy that often a complete triad may become a "compound demiplate." This combination of compounds, already seen in several genera, is here associated with a great increase in the relative width of the ambulacra and a corresponding horizontal disposition of the triserial pore-pairs. In the only two specimens of the recent *Tripneustes esculentus* that I have examined, this complex condition is only spasmodically developed, hardly more than in gerontic examples of *Echinus esculentus*.

The two families Strongylocentrotidæ and Echinometridæ develop considerably greater complexity than those described above, and, in the case of the latter group, attain the highest degree of ambulacral specialisation found among the Euechinoidea. Strongylocentrotus, the type of the former family, has, when adult, tetrad and pentad compounds in a practically continuous series from the apex to the peristome. Just near the adoral ends of the areas a few normally "Echinoid" triads remain. LOVÉN (1875, Plate 17) has described a series of ontogenetic stages in "*Toxopneustes*" *drocbachiensis*. At 3 mm. diameter the adoral half of the ambulacrum is built of triads, succeeded adapically by one tetrad, one pentad, and a few uncombined primaries. In later stages all fresh compounds in this species are pentads; hexads occur in some others. As development proceeds the primitive triads lose all visible traces of the sutures of their components, although in most cases the original elements can still be distinguished by their diverse optical orientation. Here, as in many other genera, ontogeny shows the morphogenetic relation between polysynthetic compounds and the simpler types. The ambulacrum of Strongylocentrotus may be considered to bear the same relation to that of Echinus as the tetrads and pentads of Tetrapygus do to the triads of Cœlopleurus.

The four genera of the Echinometridæ, Parasalenia, Echinometra, Heterocentrotus, and Colobocentrotus (omitting the doubtfully placed Stomopneustes) present an interesting sequence of ambulacral specialisation. I have not examined specimens of Parasalenia, but to judge from the figures given by COTTREAU (1913, Plate 2) of *P. fontannesi*, that species seems to have strongly arcuate triads throughout the ambulacra. If this is a constant feature, Parasalenia is evidently the simplest, as it is the earliest of the Echinometridæ. In *Echinometra lucunter* (Plate 63, fig. 3), the compound plates on the adapical surface are usually made of five elements, including two primaries along the apicad and orad margins. Below the ambitus most of the compounds are tetrads, but just near the peristome there are indications of the existence of "Echinoid" triads. Echinometra is thus closely comparable with Strongylocentrotus as regards its ambulacral structure and morphogeny. In *Heterocentrotus mammillatus* (Plate 64, figs. 1–5) the enormously high compounds with their arcuate pore-series are built of varying numbers of elements, but always

include two primaries (which may become almost or quite occluded locally) in the "Echinoid" position. In the gerontic specimen figured the highest compound at the mid-zone consists of 18 plates, while the average number of elements to a compound is about 11. The construction of the plates is more fully discussed in Section 2 (d), below, but it may be remarked here that there is some reason to suppose that these elaborate compounds owe much of their complexity to the union of two somewhat modified "Strongylocentrotid" pentads. The demi-plates all meet under the mamelons of the main tubercules (except adapically), whose unsutured and compact substance clearly serves to reinforce the lath-like plates at their place of union. Near the peristome the pore-fields broaden at the expense of the perradial tracts, and the arcs of pores take on an almost horizontal disposition. There are rarely any primary plates left in that region, all being compressed into included, occluded, or demi-plates. Some of the plates occasionally become so reduced that their pore-pairs may be obsolete or entirely absent. In *Colobocentrotus atratus* (Plate 64, fig. 6) the plating is essentially similar to that just described, but the average number of plates in a compound is nine. There is a far greater displacement of the pore-pairs, the arcs being practically biserial adapically, and an almost "phyllodal" arrangement obtaining near the peristome.

It would be difficult to find a more complete contrast than that between the ambulacra of the genera last mentioned and those of Bothriocidaris. Nevertheless, in Colobocentrotus, and still more in Heterocentrotus, the proportions of the polysynthetic compounds are not very different from those of the simple plates of the Ordovician prototype; while the compounds alternate more or less regularly with the contiguous interambulacrals. With the reduction of sutural tissue and the reinforcement due to the tubercles, the compounds are mechanically at least as strong as the high, hexagonal primaries. They may be actually stronger, for the calcite of the components is not all orientated the same way, so that there are no straight cleavage-lines across the compound plates. With the displacement of the pore-pairs from straight lines, the strain on the plates becomes fairly evenly distributed. By virtue of their efficient ambulacral structure, the Echinometridæ can successfully withstand the onslaught of the wildest breakers, and seem deliberately to select the most exposed reefs for their abode. So that in this family the problem of multiplication of podia without accompanying weakness of the corona has been solved, and solved triumphantly.

## (2) The Character and Significance of Ambulacral Complexity.

### (a) *Terminology.*

In the course of the work upon which this paper is based, it has been found necessary to introduce a few terms in addition to those already in use, and to re-define others with greater precision. The Echinoid ambulacrum has usually been studied

as a belt of pores, tubercles, and granules, rather than as a region of special plating-structure, and the terminology employed by the relatively few authors who have taken the latter view is in some respects inadequate. As far as concerns the terms already in use, the standard fixed by BATHER (1909, pp. 61–62) is here followed. That, as well as the original terminology of DUNCAN, and new expressions here introduced, may be briefly summarised as follows :—

(i) An ambulacrum (or ambulacral area) consists of two columns of plates called ambulacrals (or ambulacral plates) in the Euechinoidea. The columns are styled *a* and *b* in accordance with LOVÉN'S orientation (LOVÉN, 1875). The ambulacrals are numbered 1, 2, 3, etc, counting from the border of the peristome adapically. (Ideally, plate 1 should be the original member of a column, but in cases where resorption occurs during ontogeny, the proximal remaining plate must receive this number, in default of evidence as to the exact number lost.) When compound plates occur they may be similarly designated A, B, C, etc. Each ambulacral is normally perforated by a pore-pair (often enclosed in a peripodium). The belt of pore-pairs extending down an ambulacral column is called the pore-field, or poriferous-tract. If the pore-field is occupied by a continuous series of directly superposed pore-pairs, the latter are said to be uniserial. If the pore-pairs are arranged in obliquely transverse series, they are described as biserial, triserial, and multiserial, according to their grouping. If they form curved belts partially enwrapping the bases of large tubercles, they are arcuate.

(ii) An ambulacrum possesses three main sutures : the adradial (where the ambulacrals meet the contiguous interambulacrum); the perradial (the line of contact between the two columns of an area); and the transverse, which separates the plates in each column. Every ambulacral that extends across the full breadth of a column will normally possess five sutures : the adoral-transverse, adradial, adapical-transverse, apicad-perradial, and orad-perradial. For the sake of brevity, the double terms may be reduced by the omission of the words " transverse " and " perradial."

(iii) Ambulacrals may be (A) simple, grouped or compound ; (B) primary or reduced.

(A) A simple ambulacral is usually a primary, and so has the five sutural margins noted above. Even if it should be reduced, it is suturally independent of the contiguous plates. Grouped ambulacrals are those which are associated into potential compounds, but lack the intimate sutural union that characterises those structures. They are intrinsically simple. A compound ambulacral usually resembles a simple one in its sutural boundaries, but consists of two or more ambulacrals firmly bound together by a reduction of the amount of sutural tissue between them (in extreme cases by anchylosis), the whole functioning as a multiporous individual plate. There is frequently a large tubercle on each compound, so situated as to reinforce the union of the components, but such tubercles are not invariably present. If two (or more) compounds become united in a manner similar to that by which they are formed from

simple plates, the result may be termed a super-compound. According to the number of ambulacrals incorporated, compounds may be described as dyads, triads, tetrads, pentads, etc. Compounds may be built entirely of either primary or reduced plates, but usually include both types. A complete compound plate may occasionally become reduced.

(B) A primary ambulacral is one which extends from the perradial to the adradial sutures of its area (*i.e.*, across the whole width of its column). It may be a simple plate, or may be part of a compound. A reduced ambulacral is one which does not extend across the whole width of its column. There are three types of reduced plates :—($\alpha$) Demi-plates, which have an adradial suture, but no perradial ones; ($\beta$) occluded plates, which take part in the perradial suture, but do not reach the adradial; and ($\gamma$) included plates (*endoplaques* of LAMBERT) which touch neither the adradial nor the perradial sutures, and are bounded by curved transverse sutures only. For some Palæozoic Echinoidea, the term klasma-plates is applied to the polygonal ambulacrals that agree with included plates in their relation to the longitudinal sutures of the areas. Whether the plates of the multi-columnar Palæozoic ambulacra are homologous or not with the reduced plates of elaborate Euechinoid areas, they are so different in shape and disposition that the use of a distinct term is necessary for the latter structures. Reduced plates are commonly united (with or without primaries) into compound ambulacrals, but they need not be so combined.

(iv) Ambulacral plate-complexity is considered to occur (A) when the transverse sutures of simple plates are not straight, or are deflected from a horizontal direction, (B) when compound plates are developed, and (C) when reduced ambulacrals appear. The term is intentionally vague, and does not presuppose any one determinant, or crushing due to any one cause or set of causes. For the Euechinoidea, it may be employed as a general term to express the condition of ambulacra which are unlike those of the Bothriocidaroida or simpler Cidaroida. The significance of the term is further discussed in the following section.

### (b) *The Origin of Compound Ambulacral Plates.*

In the analysis of ambulacral terminology given above, one matter is involved which demands fuller consideration. It will be noticed that the phenomenon of "plate-crushing" is regarded as independent of, though often involved in, the process of the building of compound plates. The importance of maintaining this distinction is best illustrated by reference to a controversy which loses all meaning when the difference between combined plates and those which are merely grouped, distorted, or reduced is recognised. DUNCAN, to whom the first satisfactory account of elaborate ambulacral structure is to be credited, regarded the production of distorted and reduced ambulacrals as caused solely by "growth-pressure." It is possible that he included in that expression the pressure due to the expansion of

individual plates subsequent to their inception; but undoubtedly the chief type of "growth-pressure" to which he referred was that exercised by the production of new plates at the ocular-margins, and the consequent orad shifting of the columns. Dealing only with the Regular Echinoids, DUNCAN found one coincidence that naturally confirmed him in his view. The Cidaroida, in which the advancing ambulacrals can pass on to the peristome-membrane, undergoing resorption and redeposition in the process, show little or no distortion of the plates. The Diademoida, in which the development of the perignathic processes on the proximal ambulacrals demands stability in the latter, almost invariably show some degree of complexity. In the former case, the newly formed ambulacrals press against a yielding and movable column of plates; in the latter, against a column rigidly fixed adorally. It may be assumed that a mechanical explanation at once so obvious and so inevitable, must contain a large element of truth. LOVÉN, who frequently differed from DUNCAN in the interpretation of Echinoid structures, was completely in agreement with him in this matter. BATHER (1909, pp. 253–254) also expresses his belief in the influence of this type of growth-pressure on the production of complex ambulacral structure.

In the course of research into the ambulacral characters of the Irregular Echinoids, I have never found any reason to doubt the accuracy and adequacy of DUNCAN'S explanation of the origin of reduced plates. On the contrary, in every case where complex ambulacral plating has been observed, his contention has been confirmed, and no alternative has seemed possible. So complete has been, and is, my belief in the power of "growth-pressure" (in DUNCAN'S sense) for the production of elaborate plating in ambulacra, and even in interambulacra (HAWKINS, 1916), that I have been sceptical of the existence of any other force that could be so employed.

LAMBERT (1900), in the course of a study of the earlier Diademoida, put forward the view that compound plates are due to the influence of large tubercles overlapping the sutures. As far as the Diademoida alone are concerned, this explanation is fully as reasonable as that of DUNCAN. In the Cidaroida there are no large tubercles on the ambulacra, and no compound plates occur. Indeed, in one respect, LAMBERT'S view receives greater support from the Diademoid structures than does that of DUNCAN. In such forms as Hemicidaris, the non-tuberculate adapical parts of the ambulacra are built of primaries, and the production of compound plates practically coincides with the appearance of large tubercles near the ambitus. On the other hand, the adapical parts of the ambulacra of Heterocentrotus (Plate 64, fig. 1) show a degree of complexity quite disproportionate to the size of the tubercles.

In the course of investigation into ambulacral structure, two very constant features have compelled me to adhere to DUNCAN'S explanation, and to doubt the importance of tubercle-growth as a factor in the production of complexity. The first quality, which is noticeable chiefly in Diademoid ambulacra, is the tendency of the sutures to *converge* towards the tubercle. This character, which is quite

apparent in "Diademoid" triads, becomes most impressive in such polysynthetic compounds as those of Heterocentrotus (Plate 64, fig. 2). The tubercles attract, rather than repel, the sutural lines. Such a condition is incompatible with the view that the growing tubercles exert any kind of "pressure," whereby the plates on which they stand increase in area at the expense of their neighbours. The second character appears chiefly among the Irregular Echinoids. Without multiplying cases, it is sufficient to draw attention to the unusual complexity of structure in the anterior petal of Echinocardium (see HAWKINS, 1913, and Plate 69, figs. 4 and 5, of this paper). The granulation of that area is even finer than that of the rest of the adapical surface of the test; certainly, no excrescence worthy of the name "tertiary-tubercle" occurs there. So that it becomes obvious that plate-complexity, in a great degree of elaboration, can be developed quite independently of the presence of large tubercles.

However, with larger and more intimate acquaintance with the ambulacra of most families of Echinoidea, Regular and Irregular, I have reached the conclusion that both of the apparently contradictory explanations of complexity are correct. The distortion and reduction of plates is, in its inception at least, due to "growth-pressure" in DUNCAN'S sense. But distortion and reduction does not, of itself, produce compound plates. These are associations of reduced or unreduced, compressed or uncompressed, plates which are usually, and always primitively, grouped around, and bound together by, one or more large tubercles. Simple "growth-pressure" may cause the resorption and modification of stereom to almost any extent, but seems not to affect the thickness of interstitial sutural tissue. Indeed, if this organic film is instrumental in the growth of the plates (an undoubted fact), it will also be employed as an agent of resorption, and so must be maintained if the plates are undergoing that process. In compounds this placogenous membrane becomes so attenuated that the stereom of contiguous components is practically continuous. Indeed, near the peristome, all traces of sutures are often destroyed, a development analogous to "syzygy" uniting the compounds into apparently homogeneous plates.

Reverting to the principle of ambulacral development traced in Section 1 above, it may be stated that plate-*crushing* has for its chief purpose the accommodation of great numbers of podia within pore-fields of limited length, and incidentally the displacement of the pore-pairs from a straight line. On the other hand, plate-*combination* is designed to strengthen the intrinsically weak ambulacral areas, by a reduction of sutural tissue and a binding together of the several plates. It is clear that either of these processes may develop independently of the other, although the most efficient structures result from their united influence.

### (c) *The First Phases of Plate-complexity.*

JACKSON (1912, p. 59) has shown that the complexity of klasma-plating in Palæozoic Echinoidea is produced by a "drawing-out process of plate movement."

It is certain that this process, in its full effect, gives results that are strikingly unlike any features found among the Euechinoidea. But, in its earlier stages, the dislocating influence of "drawing-out" produces conditions which may be surprisingly like those attained in later types. For example, the ambulacral structure of *Lovenechinus missouriensis* (Plate 61, figs. 10 and 11) is locally identical with that of the anterior petal of *Echinocardium cordatum* (Plate 69, figs. 4 and 5). Again, the triple grouping of the ambulacrals in Lepidocidaris (Plate 61, figs. 15 and 16) results in an arrangement differing merely in the proportions and ornament of the plates from that of the adoral parts of the areas of the Pygasteridæ. The case of Lepidocidaris seems especially noteworthy, since triple arrangement is adopted without any accompanying development of overlapping tubercles. It shows that, whether the growth of tubercles does or does not influence the association of Diademoid ambulacrals, their triad quality could have been acquired independently.

There is no trace of combination in the ambulacral plating of the Palæozoic Echinoidea. This may perhaps be due in part to the absence of large tubercles on the ambulacra. But since coronal flexibility was characteristic of the majority of the forms, dissociation rather than combination of plates would naturally be more effective. The absence of true compounds makes comparison of Palæozoic ambulacra with those of the Diademoida (other than the Echinothuriidæ) unprofitable, but makes their correspondence with complex areas in the Irregular Echinoidea the more striking. In addition to the two cases of resemblance mentioned in the preceding paragraph, reference may be made to the similarity between the displaced triads of an advanced "Cassiduloid" phyllode (*e.g.*, Catopygus, see HAWKINS, 1911, Plate 8, fig. 9) and the klasma-plates of such a form as *Meloncchinus springeri* (JACKSON, 1912, p. 59). The two sets of structures are not quite identical, as in the previous cases, but are sufficiently alike to deserve comment. If to these agreements in complexity is added the very constant correspondence in simplicity shown by the "Bothriocidaroid" ambulacrals of parts of most non-Holectypoid Irregular ambulacra, the conclusion seems inevitable that there is some morphogenetic link between the two series of structures. This is probably to be found in the principle of phylogerontic atavism. The later Spatangidæ owe most of their characters to degeneration, or at least reduction, when their Cidaroid ancestry is realised. Even their symmetry may be compared, superficially, with that of a "Dipleurula," and their habits of life are not those of a robust group. Thus, if the Irregular Echinoids represent a course of evolution descending from the acme of the class, their ambulacra would naturally tend to show morpho-gerontic features, and so to revert in some manner towards a more primitive structure. That this principle is involved in their retention of "Bothriocidaroid" plates has been indicated by JACKSON (1912, p. 57), but it is peculiarly interesting to find that so elaborate a structure as that of Area III in *Echinocardium cordatum* has its prototype in Lovenechinus in the Palæozoic era. Even the relatively simple plating of the

petals of Clypeaster compares more closely with "Perischoechinoid" than Diademoid structure.

The simple primaries of the Cidaroid ambulacrum are often faintly cuneiform, but this is obviously an adaptation to the sinuous course of the area, and can be ignored in the present enquiry. Even in the Cidaroida, however, such forms as *Paracidaris florigemma* and Diplocidaris show signs of coming complexity. In Paracidaris the regular alternation of the ambulacral columns is broken at the sharper corners of the areas, and in Diplocidaris the ornament of the plates becomes diverse, finely tuberculate primaries alternating with minutely granulate ones. In the latter case it is almost permissible to regard the ambulacra as composed of grouped, though uncombined, dyads. There is no complexity in the sense of distortion of the sutures, but there is very little difference between the plating of the ambulacra of the Diplocidaridæ and those of the Saleniidæ, where dyad grouping is typical.

A very interesting and instructive account of the ambulacra of the earliest Diademoida adequately known is given by BATHER (1909, p. 254). It appears that in some Triassic types the only appreciable differences between Cidaroid and Diademoid ambulacra consist in the presence of peripodia and small tubercles on the latter. BATHER was unable to trace the transverse sutures throughout their extent, but his figures certainly justify his remark that "the plates appear equal in size." The tubercles are slightly irregular in disposition, but tend to occur on alternate ambulacrals, overlapping beyond the plates on which they are mainly based. This last character distinguishes the ambulacral structure from that of the Diplocidaridæ, but approximates it to the Saleniid type. It is worthy of note that in these forms, so far as is known, there is hardly any development of ambulacral elements in the perignathic girdle. We have, then, in the earliest known Diademoida, ambulacra that are almost perfectly Cidaroid in plating, but which show some progress in details of surface ornament.

The rarity and obscure preservation of Triassic and Liassic Echinoids make them the least known faunal series in the class, and, in spite of the work of BATHER and LAMBERT (1900), there is not yet available much material for a study of the chronological beginnings of plate-complexity. It may, however, be inferred that the Triassic ambulacra, though not comprising distorted or compound plates, show a condition that would easily resolve itself into the formation of dyads. The very constant occurrence of this simplest type of grouping in the small and retarded Saleniidæ lends support to the belief that the earliest phase of complication united the ambulacrals into pairs of primaries. In Acrosalenia the greater part of the ambulacrum is made up of alternate dyads and simple primaries. The introduction of the intervening simple plates is difficult to account for, but a similar condition at a further stage of complexity is seen in Tetrapygus and perhaps in Heterocentrotus (see p. 414). By the association of the simple plates with one or other of the contiguous compounds, triads would result. In Noetlingia, which is probably

regressive in ambulacral structure, the dyads persist, and the odd simple plates are growing obsolete. JACKSON (1912, p. 117) records as regressive variants two specimens of *Echinus affinis*, in which the apicad portions of the ambulacra are built of dyads.

For Echinoids generally, both Regular and Irregular types, triads are the predominant kinds of compound plates. In the Irregular forms, save for obviously secondary developments in the petals of some genera, a triad character may be said to be universal, although true combination is never found. A deduction from this fact would suggest that the Exocyclic Echinoidea were not differentiated from their Endocyclic ancestors before the latter had attained the "triad-stage" of ambulacral specialisation.

*Tetrapygus niger* (Plate 63, fig. 1) shows clearly the gradual production of tetrads from an arrangement of alternate triads and simple plates. It seems reasonable to postulate that more elaborate compound plates are similarly developed by the accretion of previously independent plates to already compound nuclei. The teratological specimen of *Echinus esculentus* described below (Section 2 (d), Plate 63, figs. 8, 11, and 13) is particularly interesting in this connection. Where supernumerary plates appear *between* the compounds they fail to become united with their neighbours, and are apparently gradually resorbed (figs. 8 and 11). Where such a plate has been developed *within* a compound it becomes incorporated into it by true combination, producing a "Strongylocentrotid" tetrad instead of the normal "Echinoid" triad.

In the examination of recent material it is relatively easy to determine the quality of the sutures between ambulacral plates. When the corona has been stained and etched, the unreduced sutures stand out as marked lines intensely coloured, while those separating the components of a true compound plate are either excessively delicate or are indicated by differences of the stereom mesh only. But in the case of fossil material, it is almost impossible to be certain of the nature of a suture. I am of the opinion that the sutures within compound plates in fossils are never displayed by natural or artificial etching, and can only be recognised by their influence on surface relief or ornament. On the other hand, the normal sutures that separate simple or compound plates, being filled in by a secondary mineral film, are liable to be made apparent by differential solution, preferably by the weather. Such satisfactory preparation of the specimen must inevitably be rare; and it is generally restricted to small regions in any one corona.

Examples of Diplopodia and Stomechinus that have undergone natural etching have convinced me that the presence of tubercles extending across more than one plate is not a certain indication of true combination. In both these genera all the ambulacral sutures near the apex seem to have the same width and "solubility," although the plates are well grouped into triads or more elaborate associations with superimposed tubercules. Towards the ambitus and adorally, only the main sutures seem capable of exposure by solution, so that there true compounds may be presumed to exist.

In the least elaborate, and chronologically earliest, types of compound plates, whether dyads or triads, the components are always primaries. It is therefore safe to assume that plate reduction did not appear before compound plates had been evolved. In a normal "Diademoid" triad the three primary components are not equal in size, nor are their transverse sutures straight, but their departure from simplicity is not associated with appreciable reduction in their average area. They are not *crushed* plates in any sense of the word. Rather the arcuate nature of their transverse sutures seems to indicate a convergence towards the tubercles of the compounds so that they may benefit by the cementing influence of the compact stereom of the mamelons. An additional determinant may be the departure from uniserial arrangement of the pore-pairs.

In the Regular Echinoids that retain some degree of simplicity in their ambulacra, the first indication of "crushing" always occurs near the adoral ends of the areas. This does not imply that the compound plates of those regions are more elaborate than elsewhere (the reverse is the case), but that their components are there distorted or reduced. This condition is most clearly seen in the simple Diademoida, such as Hemicidaris, in which the supra-ambital ambulacrals are practically Cidaroid, but it is none the less made manifest in more advanced types by the intensity of pore-congestion towards the peristome. It is thus safe to assume that the first *place* for the development of plate-complexity in Regular ambulacra is near to the adoral extremities of the areas. From that region the effect of crushing may extend adapically (both in ontogeny and phylogeny) until there is not a simple ambulacral left in the area. Indeed, in the Echinidæ and Echinometridæ, many of the new plates developed at the oculo-ambulacral suture seem fore-doomed to reduction, and never take on a simple character. This acceleration of the development of reduced plates in late post-larval growth in highly specialised types is strictly analogous morphogenetically to the introduction of elaboration into early larval ontogeny recognised by BEECHER.

### (d) *The Capacity and Limits of Plate-complexity.*

(i) *The Production of Reduced Plates.*—DUNCAN was the first to recognise and classify the types of arrangement that occur in compound ambulacrals in the Regular Echinoidea. Three of the chief groupings of components are modifications of triads: the Diademoid, Arbacioid, and Echinoid types. It will tend towards clearness in the succeeding arguments if the interrelation of these three styles of combination is first considered.

The chronologically earliest, and morphologically simplest, type of triad is the Diademoid, in which the three components are all primaries, with a tendency for the apicad and orad plates to be lowered ad- and per-radially, and for the median plate to be consequently hour-glass shaped. The boss of the tubercle (when one is present)

is situated on the median plate, and its scrobicule extends across the reduced sutures on to the other two components. This character is certainly of common occurrence in the Diadematidæ, but is rarely maintained without modification in most genera of that family. Towards the peristome one or both of the external components become separated from the perradial suture, as a result of excessive lowering of the perradial parts of the plates. There is thus developed a more or less complete approximation to the Arbacioid type. In that class of triad the median component, while low adradially, becomes relatively very high perradially, and alone possesses the perradial sutures of the compound. The apicad and orad plates are reduced into demi-plates. In the majority of cases these demi-plates do not taper away gradually in a perradial direction, but retain their full height until they reach the tubercle, and then are abruptly truncated, their sutures turning through a right, or even an acute, angle. The perradial expansion of the median component is not, therefore, due to the extension of the tubercle, but is probably to be ascribed to the need for a reduction in the quantity of suturing in the area. The position of the tubercle and of the perradiad limits of the demi-plates suggests that their coincidence is not accidental, but that the tubercle binds the three components together as in the Diademoid triads.

The derivation of the Arbacioid type of compound from the Diademoid scarcely requires argument: not only is it the logical sequel to the tendency started in the latter type, but within the limits of a single area the transition can be traced. The type may be elaborated in two different ways. In Arbacia itself, and in such forms as Tetrapygus and Goniopygus, tetrads or more complex compounds may be developed by the incorporation of new plates introduced *between* the original triads; much in the same way that the triads themselves probably originated from alternate dyads and simple plates. In such genera as Leptarbacia (Plate 62, fig. 16) and Pedinopsis, this process seems clearly indicated, and to judge from the figures of the former given by Clark and Twitchell, the resulting tetrads and pentads are not truly combined adapically. At least the compounds have ill-defined transverse sutures, similar to those in the adapical parts of the areas of Tetrapygus (Plate 63, fig. 1). In the latter case, the extra plates may be traced adorally, and are seen to enter gradually into true combination. The other type of elaboration is shown in its extreme development by the "Phymosomoid" compound, where hexads and occasionally heptads are formed by the introduction of extra demi-plates *within* the body of the compounds. This type leaves the two external components in their "Arbacioid" or sometimes "Diademoid" relations. The same method is employed in the more elaborate derivations of the Echinoid type.

The Arbacioid type is certainly older, and apparently simpler than the Echinoid. In the latter a completely contrasted structure is seen, for the median plate becomes reduced to a demi-plate (usually of very small dimensions), while the adapical and adoral components tend to retain their primary character. In the majority of cases,

a fully developed Echinoid triad consists of a broad low apicad demi-plate, a minute median demi-plate projecting somewhat into the interambulacrum, and an orad primary which extends for the whole height of the compound in the perradial tract (see Plate 63, fig. 2).

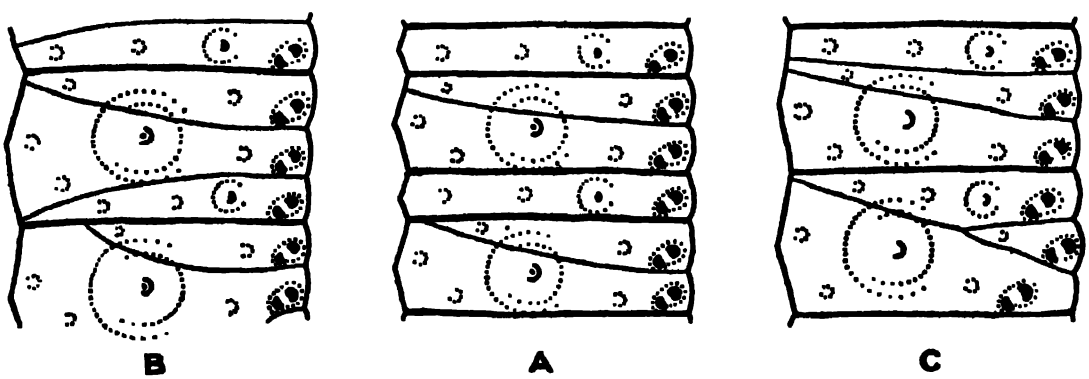
Starting from a normal Diademoid triad, with a centrally constricted median component, it is easy to imagine that further constriction would cause the transverse sutures of the median plate to meet. Such a phenomenon would produce an adradiad demi-plate, but would also leave a perradiad, imperforate occluded portion. Such a feature does not occur in reality—I have never seen even a teratological specimen with such an anomaly. Hence, if the median demi-plate has been produced in the manner above indicated, the greater part of the adoral transverse suture of the median plate (*i.e.*, of the adapical transverse suture of the adoral plate) must have entirely disappeared. The other possible interpretation of the median demi-plate is that its bounding sutures, and the single suture which extends from it perradially, are actually the complete two sutures of the original median primary, that plate having become lowered to the degree of extinction in its perradial portion. Such a hypothesis would involve a complete reversal of the Diademoid tendency, and is thus improbable.

Assuming that the former suggestion as to the origin of the demi-plate is correct, it would be expected that some evidence of its truth might occur in teratological, if not in normal cases. The large and otherwise perfectly normal specimen of *Echinus esculentus* from which Plate 63, fig. 10, has been drawn, seems to supply such evidence. Occasional triads are still in the retarded (or regressive) Diademoid condition, with the constriction of the median plate strongly marked. A considerable sequence of compounds in the same area are, as it were, upside down in structure. The transverse suture which separates the two external components slopes adorally instead of adapically, sometimes reducing the orad component to the condition of a demi-plate, leaving the entire perradial suture to the apicad component. Here, surely, for some inexplicable reason, the adapical transverse suture of the median "Diademoid" plate (*i.e.*, the adoral transverse suture of the apicad plate) has disappeared. Plate 63, fig. 10, in which three separate compounds from one column are placed together, shows more clearly than any further description the apparent relation between Diademoid and Echinoid triads.

The importance of this argument lies in its corollary. In the majority of Regular Echinoidea the compound plates owe some of their character to the destruction of part of a suture. Hence, if the argument is sound, plate-complexity is capable of obliterating sutures. This is not quite comparable with the "syzygous" union of some plates near the peristome in many advanced Regular forms, for there it is usually possible to trace the original limits of the components by the optic orientation of their calcite or by differences in the stereom-mesh. No such tests resolve the surviving primary of an Echinoid triad. The fact that the morphoneanic plates at

the apicad ends of the ambulacra in such advanced genera as Echinus or Heterocentrotus are developed in a reduced state is probably due to accelerated and compressed recapitulation, in which the stages in the attainment of the reduction have been omitted. In this connection it is appropriate to refer to the existence of the "biporous ambulacrals" around the Spatangid peristome. The principle enunciated above implies that it is *possible* that these might originally have been two plates, although it would be premature to attempt any conclusion on the subject here.

There is another possible method of derivation of the Echinoid triad which, though morphologically simple, seems less in accord with observed facts than the one indicated above. It is at least probable that the Diademoid triad was developed by the addition of an intervening simple plate to a Saleniid type of dyad. In such a primitive compound, the apicad member of the pair is usually the smaller, and may occasionally be reduced. If the intercalated plate were to become combined with the dyad *adapical* to it (and to undergo the reduction which commonly befalls such plates), an approximately Arbacioid triad would result. If, on the other hand, the extra plate were to be attached to the dyad *adoral* to it, an Echinoid triad would inevitably be produced. The very constant reduction of the apicad component of an Echinoid triad, though less in degree than that suffered by the median plate, would be in accord with such a theoretical origin for the compound. Text-fig. 1 shows in




TEXT-FIG. 1.—Diagram showing a possible (but improbable) method of derivation of the Arbacioid (B) and Echinoid (C) types of triads from the Acrosaleniid (A) condition of alternating dyads and monads. All the figures show a progressive increase in elaboration from above downwards.

diagrammatic fashion the possible derivation of the three types of triads from an Acrosaleniid condition of alternate dyads and simple plates. There are, however, two serious difficulties involved in such an explanation. Firstly, the Arbacioid structure may be, and often is, derived *through* the Diademoid, and so need not be traced back to the Acrosaleniid type; while the frequent abnormalities found in Echinoid triads illustrated in Plate 63, fig. 10, are only intelligible if taken as regressive variants pointing to a Diademoid origin for the compounds. Secondly, the Echinoid type of triad seems not to have appeared before Cretaceous times, while the

increase from dyads to triads had been established long before that period. The question of the morphogeny of the Echinoid triad needs fuller investigation before any solution can be attempted. The problem is, however, foreign to the purposes of the present study.

Except in the ambulacra of the Echinometridæ, *occluded* plates are rarely developed among the Regular Echinoidea outside the regions of peristomial pore-crowding. They seem to be an inevitable product of complex-arcuate or highly multiserial pore-series. Such grouping causes two or more pore-pairs to occur in practically a transverse line, and the plates bearing the perradial pores have perforce to disappear before reaching the adradial suture. Even so, it is remarkable how the plates of the inner series seem to cling to the adradial suture, although they may be reduced to strips of calcite of hardly greater height than that of the sutural tissue. In the phyllodes of the "Cassiduloida" (*sens. lat.*) such occluded plates are commonly found, and they form an important proportion of the elaborate anterior petal of *Echinocardium cordatum*.

*Included*-plates are still more exceptional among the Regular Echinoidea. They may be defined as demi-plates which have become occluded. The aberrant genus Noetlingia and the Echinothuriidæ are the only types in which such plates constitute an important part of the ambulacra. They occur sporadically in Heterocentrotus, especially towards the peristome. In the petal of area III of *E. cordatum* they are present in considerable numbers. It is often to be noticed that the pore-pairs of included plates differ somewhat from those of the rest of the ambulacrum, usually in the direction of less complete development.

The essential difference between demi-plates and the two types just described consists in their relation to pore-crowding. Demi-plates are often present when there is little or no congestion of the pores (*e.g.*, Phymosoma), and hardly any decrease in their vertical inverval. On the other hand, occluded and included plates are always restricted to those areas or parts of areas where serious displacement of the pores, and diminution in the height of the plates, are found. In other words, demi-plates are often adaptations for the strengthening of ambulacra by reduction in the amount of sutural tissue; occluded and included plates for the multiplication of podia. The latter types are therefore to be ascribed to "plate-crushing" in its literal sense.

In this connection a fresh question arises. If plates can be materially reduced in size by crushing, can this process be carried to its extreme, and plates, with their podia, be crushed out of existence (*i.e.*, totally resorbed)? Such a process would, in some measure, be an over-specialisation, since the crushing that might achieve it seems designed to multiply, not to reduce, the number of pore-pairs. Nevertheless, there seems to be substantial evidence in favour of the view that ambulacrals may be obliterated by crushing. In the large and otherwise normal *Echinus esculentus* described below (Plate 63, fig. 14), certain pore-pairs are situated well out in the

interambulacra near the ambitus in two of the areas. In every case these displaced pore-pairs belong to the median demi-plates of the triads. In some of the compounds affected the demi-plates are very minute, quite imperforate, and strongly projecting beyond the normal line of the adradial suture. In one case the demi-plate is absent, the compound being built of the apicad and orad members only. In this case, although the podia have survived, the condition suggests that some of the reduced ambulacrals have undergone more or less complete resorption on account of abnormally intense crushing. In the specimen shown in Plate 63, fig. 12, a whole triad shows signs of approaching destruction.

In *Noetlingia boulei* (Plate 63, figs. 4 and 5), according to LAMBERT (1906, p. 11), the adoral parts of the ambulacra consist of dyads (with an apicad demi-plate) alternating with variously distorted simple plates. At and above the ambitus the dyads are maintained almost unaltered, but the alternating "monads" are reduced to very small included plates. The suggestion made above (p. 392), that these intervening plates, having missed incorporation with the compounds (otherwise normal Echinoid triads might have resulted), prove out of harmony with the system of plating adopted, and tend to become obsolete—seems consistent with the evidence afforded by the abnormal Echinus shortly to be described. The pore-pairs that perforate the included plates are so minute that NOETLING (1897, p. 15), in founding the genus (*subnomine* Protechinus), remarked that "the pores are seemingly arranged in groups of two . . .; the third pair, however, is so much reduced that it is hardly visible." Later he uses the term "obsolete" to describe the condition of the included pore-pairs. In Noetlingia, then, there seems reason to believe that one set of plates, together with its series of podia, is in process of destruction.

Lastly, in the gerontic Heterocentrotus described below, there are in some of the compounds undoubted included plates which are so reduced that they do not extend beyond the bosses of the tubercles, and are quite imperforate. Other included plates of rather more complete preservation show the pore-pairs in various stages of resorption or blocking.

In view of these facts, it seems legitimate to propound a second principle, viz., that plate-crushing is capable of obliterating ambulacral plates, with or without the corresponding destruction of their podia.

The third and last phase of plate-complexity that need be mentioned here is the reduction and combination of compound plates, forming super-compounds. This condition occurs in many groups of the Diademoida, and its gradual development can be traced in the ambulacra of large specimens of *Echinus esculentus*. It represents the highest type of ambulacral complexity, although a super-compound of one genus need not include as many pore-pairs as a normal compound of another. I have never seen a case where more than two compounds become united, but there seems no reason to doubt the possibility of the occurrence of "super-triads."

(ii) *Detailed Description of the Structure of the Ambulacra in Echinus and*

*Heterocentrotus.*—The three chief effects of plate-complexity that have been indicated in the preceding paragraphs, together with certain details of less general application, can best be illustrated by the description of definite cases of ambulacral elaboration. Whether these cases are normal or teratological is immaterial, since even disease cannot induce the development of impossible structures, and features abnormal in one group of organisms may prove to be the rule in another.

### (*a*) *Echinus esculentus.*

After the examination of several hundreds of specimens of this abundant species, from various British localities, and of sizes varying from 3 mm. to about 140 mm. in diameter, the most enduring impression gained is that of wonder at the remarkable uniformity of structure displayed in the ambulacra. When it is realised that a moderately large example has ten ambulacral columns, each composed of some 230 plates (*i.e.*, about 2,300 ambulacrals in all), grouped into about 77 compounds (*i.e.*, about 770 triads in all), the scope for variation, or at least for irregularity, in so lavish a repetition of similar structures is manifest. But specimen after specimen can be carefully studied without the discovery of any trace of abnormality in a single plate. Even in cases where some serious accident or disease has deformed or otherwise modified other coronal structures, the ambulacra are often perfectly normal. Moreover, irregularities in the disposition of the tubercles and granules of the perradial tracts are by no means always accompanied by structural disturbances. Plate 63, fig. 2, shows a typical ambulacrum drawn from a specimen of 106 mm. diameter. At the two extremities of the area the compounds are typical "Echinoid" triads in DUNCAN'S terminology, having two unequal primaries enclosing a small demi-plate. The greater part of the area is composed of plates in which the apicad primary is reduced, and, indeed, this condition deserves the name "Echinoid" more truly than the young, partially developed state found adapically and adorally. Very rarely, chiefly in the adoral region, one or both of the external members of a triad may be occluded, but the occlusion is never profound, and usually occurs on the outer surface of the test only.

It seems fitting to prefix the above remarks to the rest of this sub-section, because without them the impression might be gained that ambulacral abnormality is common in *E. esculentus*. The reverse is the case, but in a discussion of the capacities of plate-complexity, the reaction to cases of irregularity demands fuller description, and is more instructive.

By far the most frequent variant in triad-formation in *E. esculentus* is the inversion of the course of the median transverse suture already discussed above (see Plate 63, fig. 10). According to my experience, this abnormality is even commoner in *E. norvegicus* and *E. acutus*, but is very rare in *Parechinus miliaris*. Next in order of frequency is the reversionary "Diademoid" plate, in which the resulting structure sometimes has partly "Arbacioid" characters. These two relatively unimportant

variations very commonly occur in areas that include more profound abnormality, but they may be independent of any such disturbing influence. They may appear in any part of a column, and their development in one area or column does not necessarily imply that they are to be found in other areas of the same corona. In no case have "Diademoid" or "inverted" triads proved to be associated with irregularity in the disposition of the pore-pairs, and they certainly do not involve either greater or less compression than that exercised upon normal compounds. Finally, neither type need show any discrepancy in ornament from the others. Both are best intelligible if regarded as manifestations of morphogenetic atavism, the regression being often instigated by the existence of some other irregularity of development.

Plate 63, figs. 6 and 7 illustrate the gradual production of super-compounds (akin to those of Astropyga) at the mid-zone in gerontic specimens. The example shown in the former figure is actually somewhat precocious in this respect. It is only 70 mm. in diameter, while the stage of "super-combination" that it has reached is usually not attained until the diameter is about 90 mm. The gradual production of compound demi-plates, and the influence (if any) of the major tubercles on the process, are so plainly shown by a comparison of the figures that further verbal description is unnecessary.

Turning now to cases of true abnormality; a few types have been selected as showing features helpful to the present discussion. All cases due to repair of injury, or associated with other coronal abnormality, have been excluded. Of the figures given in this connection, four (Plate 63, figs. 8, 9, 11, and 13) are drawn from the ambulacra of a single specimen. Unfortunately the corona (from Port Erin, Isle of Man) had undergone very rough treatment before I acquired it. It was one of a set exhibited for sale to tourists, and had been scraped with a knife to remove the radioles, with the result that most of the tubercles are broken. Also, the contents of the test had been violently extracted through the peristome with the same implement, so that the ambulacra are incomplete adorally. Hence it is impossible to attach their correct numbers to the plates. Beyond a reconstruction of the broken tubercles (whose bases were still apparent) there is nothing in the figures that is not perfectly clear in the specimen.

Fig. 8 shows a portion of area IV about midway between the ocular plate and the ambitus. In column *a* one, and in column *b* two contiguous, supernumerary plates occur between the normal triads. These plates, as the nature of their sutures shows, are in no way combined with their neighbours, nor (in column *b*) with one another. All are reduced to demi-plates, and the apicad supernumerary in *b* has a distinctly smaller pore-pairs than usual. It is noteworthy that in all three cases the pore-pairs are situated well away from the adradial suture, although normally the peripodia of the demi-plates impinge upon that line. There seems to have been a spasmodic increase in the rate of production of new plates at the ocular margin, so that some were built in excess of the requirements of the triads. In their subsequent

history, these extra plates have become reduced, and seem threatened with resorption. It may be surmised that, had such a development occurred in a type less established than Echinus, tetrads might have been formed; and such a modification might well have come to be adopted as a permanent feature.

Fig. 9 (Plate 63) illustrates the condition of area I in the same specimen, at about the same horizon of the corona. Column *b* is here perfectly normal, but two aberrant features occur in column *a*. At X there is an intercalated demi-plate precisely similar to that of column *a* in area IV. At X′ a very curious modification appears. At first sight the three plates marked seem to constitute an "Arbacioid" triad. Actually, however, the three plates are quite uncombined. Here a disturbance in the sequence of plate development at the ocular has resulted in an attempted "parallel variant" in the Arbacioid line. But, owing to their incongruous disposition, the plates have failed to unite into a compound.

Fig. 11, from area I below the ambitus, shows perhaps the most striking, and certainly the most interesting, of the abnormalities present in the specimen. A supernumerary, uncombined plate is *included* along one of the main transverse sutures. It is of such small dimensions that its surface is almost covered by the very reduced peripodium, while its pore-pair is almost obsolete. Occurring, as it does, below the ambitus, this plate was developed earlier in the life of the Echinus than the similarly additional plates of the adapical surface shown in figs. 8 and 9. It is reasonable to suppose that it shows the condition to which, in course of time, they would have been brought. It is evident that complete destruction of the surplus plate is imminent. Again, this small, minutely perforated, included plate, is strictly comparable with the inner series of plates in Noetlingia. The explanation of the ambulacral structure of that curious genus offered above (p. 392) is supported, if not actually confirmed, by this abnormality in Echinus.

Fig. 13, from the adoral part of area III, shows the intercalation of a surplus demi-plate at X, converting the compound into an apparently normal "Strongylocentrotid" tetrad. In this case the extra plate has definitely combined with its neighbours, but it is reduced in size, and its pore-pair is disproportionately small.

Fig. 12, which is taken from the ambital part of area III of another specimen, shows a comparable, though different, type of irregularity. At X a whole triad is in course of destruction. The two external components are both occluded, and have much reduced pore-pairs, while even the demi-plate is adradially lowered in comparison with those of normal triads. On counting the plates in the two columns of the area, it is found that *a* has three more than *b* (214 and 211 respectively). There is thus one triad too many in column *a*, and the one figured seems to have been selected for resorption so that plating and pressure may be equalised.

By far the most interesting abnormality that I have seen in the ambulacra of *E. esculentus* is that illustrated in Plate 63, fig. 14. While bearing some resemblance to that described by CHADWICK (1914), it differs in the otherwise complete regularity

of the corona. The specimen (in the collection of Ll. TREACHER, Esq., F.G.S.) is a large one of about 120 mm. diameter, and is slightly more thickly tuberculate than usual. Areas II and IV both have extraordinarily congested pore-fields, the development of ambulacral plates having been abnormally rapid. A portion of area IV from the ambitus towards the peristome is here figured; the corresponding section of area II is essentially similar in character. In column *a*, plate 57 to 65, are normally combined into three triads. The "triad" 66–68 contains two plates only—the median demi-plate (67) is wanting. But out in the interambulacrum, at a distance from the adradial suture greater than the width of the pore-field, there is a pore-pair differing from the normal merely in size, position, and the absence of a peripodium. The next triad is normal, except that the apical component is occluded. Compound 72–74 has the median demi-plate much reduced, and its pore-pair, failing to find accommodation in its normal position, is partly in the interambulacrum. The next triad is inverted and the succeeding one normal. Triad 81-83 is inverted, and the small median plate projects far out interradially; perhaps the incidence of the transverse interambulacral suture encouraged this displacement. After the next four triads (normal, inverted, normal, normal), plate 96–98 shows a condition like that of 72-74, but here the demi-plate retains its full breadth. The decrease in its height has driven the pore-pair across the adradial suture. Several occluded plates occur in the column between Nos. 105 and 111.

In column *b*, plate 64–66, has a minute imperforate demi-plate, whose pore-pair is well out among the interradial tubercles. Plate 112–114 shows the condition found twice in the adjacent column, the reduced demi-plate being insufficient to contain the whole of its pore-pair. An anomaly in the numbering of the plates will be noted. While in both columns plates 57 are very nearly on the same horizon, plate 112 of column *a* is considerably lower (*i.e.*, nearer the peristome) than the corresponding plate in *b*. This means that there are more plates in *a* than in *b* in the region figured. The extra plates seem to exist in the whole triad 108-110, where a condition of occlusion precisely like that shown in Plate 63, fig. 12 occurs, except for the maintenance of the size of the pore-pairs. It is noteworthy that there are three pore-pairs displaced in *a*, and only two in *b*.

In this most remarkable specimen, unusual rapidity of plate development in two ambulacra is manifest in the crowding of their pores. The consequence has been an exertion of "growth-pressure" (in DUNCAN'S sense) to an unusual degree. This pressure has not reduced the size of the pore-pairs, but has disorganised the plates. Those ambulacrals in which the peripodia are normally perradial in position have frequently become occluded, and those with adradial pore-pairs have been more or less extruded from the area. These demi-plates are so reduced that they cannot contain their pore-pairs, and in one case a plate, of whose previous existence there can be no reasonable doubt, has totally disappeared. The influence of "growth-pressure" is surely indicated here; no other explanation of the phenomena seems possible. The

interambulacral position of the extruded pore-pairs is particularly interesting in view of the normal extension of podia over the interambulacra in the Clypeastroida.

### (β) *Heterocentrotus mammillatus.*

An unusually large, gerontic individual of this species has enabled me to trace the later phases of complication in an ambulacrum which is the most highly specialised known among Regular Echinoidea. The test of the specimen is exceedingly thick; and, since it readily separated into its component plates, it has been possible to compare the arrangement of the plate-sutures on both sides of the corona, and to trace their course across the adradial suture-face. Stereo-sections have been prepared of various fragments, so that the appearances on the surface have been checked by a study of the stereom-mesh and of the optic orientation of the plates.

The pore-pairs are arranged in strongly curved arcs (much more so externally than internally), which tend to become biserial towards the apex. The apicad and orad pores of the compounds are practically in the perradial tract except near the ambitus. Towards the peristome the pore-pairs become massed together so that the peripodia are almost in contact, and no order in their arrangement can be determined by superficial examination. The general structure of the compound plates is much elaborated beyond that of an Echinoid triad, but that basis is none the less apparent. The largest plate of a compound is the orad member, the second largest is usually the apicad (normally occluded) and the remainder are either demi-plates or included. The perradial suture is made up entirely of the edges of the two external components, as in the Echinoid triad.

In Plate 64, fig. 1, the adapical part of Ambulacrum I is drawn. In spite of appearances, the plating-structure is in many ways more complex here than lower down in the area. This point is noteworthy in view of the feeble development of the tubercles. It is difficult to define with confidence the limits of all the compounds, since the plates are, on the whole, grouped rather than combined. In column *a* the apicad compound, presumably limited adorally by the large occluded plate bearing a small tubercle, has five demi-plates in addition to the main component. The apicad margin of this column is the oculo-ambulacral suture, so that the last-formed plate is clearly a demi-plate at its inception. The succeeding compound seems to have three plates reaching the perradial suture. The small apicad occluded plate I consider to be comparable with the additional plates between the triads in Tetrapygus, while the low primary is the true apicad component. There are six demi-plates between this and the tuberculate orad primary. The next compound shows a similar supernumerary plate, followed by a much reduced occluded apicad member. The orad plate of this compound is also occluded, and ten demi-plates intervene. The characters of the fourth compound from the apex are normal, and one demi-plate has become occluded (hence being an included plate). Included plates, sometimes with obsolescent pore-pairs, begin to figure largely in the fifth compound, which is

only partly shown in the figure. Column *b* is very similar to *a*, but the second plate down seems strangely simple in composition, comprising four demi-plates only, in addition to the external components.

Fig. 2 (Plate 64) shows the mid-zone, where the large tubercles, abundant smaller ornament, and semicircular arcs of pores make up a design unrivalled for beauty among the Echinoids with which I am acquainted. The sutures are clearly visible, except on the mamelons (where they do not exist at the surface, but have been inserted on evidence supplied by sections), and the regularity of the structure is surprising, in view of its extreme complexity. Sixteen demi-plates (18 components in all) represent the fullest degree of combination in this specimen. In the largest compound of column *b*, the third demi-plate from the adoral margin has its pore-pair almost obliterated by the growth of a minor tubercle on the adradiad part of the plate. The only occluded plates in this region are the external components.

In fig. 3 the congested area of pores near the peristome is shown. Traces of sutures appear here and there among the peripodia, and show clearly on the bosses of the main and secondary tubercles. On several of the large tubercles, the outlines of included, imperforate plates are very sharply defined, but I should have hesitated to insert them had not sections confirmed this peculiar feature. Great as is the number of pore-pairs in this region, it is inferior to the number of plates; several have been lost during ontogeny. In the two lowest tubercles on which sutures can be seen, it will be noticed that there are two sutures on the perradiad sides of the bosses. Reference to fig. 5 shows that these tubercles rest upon two compound plates, thus producing more or less definite super-compounds.

In fig. 5 part of the corresponding region of another area of the specimen is shown in section. The section was taken as near to the exterior surface as the irregularities allowed. The effect of excessive crushing in the production of occluded and included plates, both with and without pores, is very clearly displayed. The influence of the tubercle as a "binder" is also obvious. The pore-pairs are seen to be disposed in double, almost transverse, arcs in each compound, and the distribution of the sutures suggests a "double Strongylocentrotid" origin for the plates. The transverse sutures, which roughly bisect each polysynthetic plate, are almost identical in character, so far as they extend, with the transverse sutures that bound the compounds. So that it is possible that a "Heterocentrotid" compound is really a more or less modified "Strongylocentrotid" super-compound.

Fig. 4 represents the surface of the greater part of the adradial suture. The main sutures of the compounds are indicated by thick lines, which are produced beyond the exterior edge, otherwise the figure is in no way diagrammatic. It will be observed that the arrangement of the sutures undergoes great alteration between the two surfaces of the test. Many plates that are demi-plates externally prove to be included internally, and some that are superficially occluded are true primaries within. On the whole, there is a tendency for a reduction in the number of plates

that reach the adradial suture internally, consequent on the curvature of the corona. This must be due to "growth-pressure"; it cannot well be caused by tubercle growth. The simple and direct course of the sutures of the proximal orad compounds, sheltered as these are behind the projecting perignathic processes, seems equally conclusive in this respect. The earliest formed plates preserved there have been protected by the process from the downward drive of the advancing column, while those near by, devoid of this shelter, are intensely crushed and deformed. The view that plate-complexity in the Diademoida is largely due to the impact of the plates upon the rigid perignathic girdle thus receives notable support.

The detailed study of the two types of ambulacra just described has supplied much of the evidence on which the preceding section was based. It also shows, to my mind, that "growth-pressure" is a real force in the determination of ambulacral complexity, although the influence of tubercles as central reinforcements in compound plates is none the less marked. Lastly, a comparison of the ambulacra of Echinus and Heterocentrotus shows that the latter are much modified developments from the former, the chief difference consisting in the incorporation of additional demi-plates within the bodies of the compounds. Phymosoma stands in a comparable relation to Diadema or Arbacia.

As a summary of the results reached in the last two sections, the following theory of the origin of ambulacral complexity may be put forward. The first phase of complication consisted in the grouping of the ambulacrals into pairs (dyads) of primaries, which gradually became combined by the transgression of tubercles over their common suture. Later, non-tuberculate simple primaries appeared alternately with the dyads, and these gradually became attached to (usually) the compound adoral to them. This produced the "Diademoid" triad, of which the "Arbacioid" is but an exaggerated type. Such triads could be amplified in two ways. In one case, further incorporation of alternating simple plates, in a manner similar to that above described, gave the "Tetrapygus" tetrads or pentads. In the other, addition of extra plates between the components of the triad resulted in the "Phymosoma" hexads or heptads. By a modification of the Diademoid triad, involving the destruction of one of the internal transverse sutures of the compound, the "Echinoid" triad arose. This type is usually complicated (when amplification occurs) by the intercalation of internal plates (after the "Phymosoma" manner), giving rise to "Strongylocentrotid" and "Heterocentrotid" polysynthetic compounds. Adapically, in Heterocentrotus, there seem to be indications of a "Tetrapygoid" addition of new plates between the compounds, but this is a very exceptional occurrence in the Echinina. The grouping or combination of the ambulacrals is often quite unassociated with any increase in the number of plates in a column, and seems designed primarily as an aid to the mechanical strength of the area. Even demi-plates are frequently manifestations of the need for suture-reduction rather than evidence of compression. On the other hand, occluded and included plates are invariably restricted to those

areas or parts of areas where the pore-pairs are congested, and their presence serves as an indication of the incidence of "growth-pressure" in its widest sense.

(e) *The Relation between Plate-structure and Function.*

The functions of the podia of the Echinoidea are various, and are probably rarely exercised singly. Perhaps their most constant purpose is to afford means for the aëration of the fluids in the vascular systems of the body. But, in the Regular Echinoidea, this possibly primitive function is more or less subordinated to the adhesive and ambulatory uses of the podia. That this adaptation was progressively acquired in the course of the specialisation of the group seems likely, and it is perhaps rendered more feasible in the Diademoida by the presumed respiratory function of the external or peristomial "branchiæ." These tufted extensions of the water-vascular system are apparently largely concerned with the regulation of hydrostatic pressure during mastication, but their branchial designation is almost certainly appropriate in some degree.

Nothing definite can be ascertained as to the chief uses of the podia of Bothriocidaris; but it may be suggested that the sparse distribution and small numbers of the "tube-feet" would not make them efficient as organs of locomotion or adhesion. In Cidaris the absence of peristomial "branchiæ" may imply that the respiratory function of the podia is of first importance; certainly the adhesive function is but feebly developed. Jackson (1914, p. 141) remarks that "in collecting Eucidaris [*tribuloides*] one simply picks them up, and in no case observed did the animal cling to the ground by its tube-feet." The same author (*loc. cit.*, p. 142), writing of *Centrechinus* [*Diadema*] *setosus*, states that "the tube-feet have only the slightest hold on the sea-floor, so that specimens can be picked up . . . without any perceptible resistance." Diadema has the peristomial "branchiæ" well-developed, so that the lack of power in its podia seems not to be attributed to their pre-occupation with a respiratory function. On the other hand, Jackson (*loc. cit.*, p. 154), referring to *Echinometra lucunter*, explains that "this species clings tenaciously to the rock, and has to be pulled off from the rock with some effort." The same remark would apply equally to Echinus or Strongylocentrotus. Although specimens can be dislodged from the rock with fair ease in a surprise attack, their power of adhesion when alarmed is such that their collection with ungloved hands is painful and uncertain. Often they will cling so tenaciously that the podia are torn asunder before the adhesive suckers give way. The inference from these observations is obvious. Those forms that can exert strong powers of adhesion are precisely those which have compound plates where the degree of combination is complete, the components are reduced, and the pore-pairs multiserial. Hence the production of compound plates, and the plate-crushing associated with multiserial pore-pairs, are adaptations towards the adhesive function of the podia. If Cidaris were to resist removal with an energy approaching that exerted by Echinus, the weak, simple ambulacrals would be torn from the corona.

So that plate-complexity, both in combination and crushing, seems to be necessary for the exercise of the most vital podial functions in forms which, like the higher Diademoida, inhabit tidal zones of the sea-floor, and, in their search for clear water, prefer wave-swept rocks where little shelter can be obtained. For such purposes, the number of podia and the strength of the ambulacra could hardly be too great; and from the Triassic period to the Holocene the record of ambulacral evolution in the Regular Echinoidea has been one of steadily progressive elaboration, culminating in the marvellous complexity of the areas in the higher Echinometridæ of the present day.

In Regular Echinoids, all the ambulacra, throughout their entire length, have much the same function and type of structure. Adhesion is practised most often in the neighbourhood of the peristome, and there the degree of plate-complexity is greatest; but the difference is in degree only. In the Irregular Echinoids a far more varied use is made of the ambulacra, in spite of the almost complete transfer of locomotor function to the radioles, and of the absence of opportunities for adhesion in a sand-burrow. Generally speaking, a characteristic ambulacrum of a mature Irregular form consists of three, sometimes of four, sections. Adapically petals are developed, and through these respiratory podia protrude. Near the peristome, phyllodes or their equivalents give passage to podia which are mainly sensory, although in the "Cassiduloida" some adhesive function seems to persist. In those advanced Spatangoida (Prymnodesminæ) which have subanal fascioles, a few long, probably prehensile, podia project from the ambulacrals thereby enclosed. For the rest, the podia are reduced to mere filaments (inevitably in some measure respiratory and sensory) which are of relatively little functional value.

It is obvious that the branchial podia of the petals are of such importance that their numbers must be maintained, and can with advantage be increased. But at the same time the exercise of their function does not involve the corona in any mechanical strain. The ambulacral plates in the petals are usually simply "Cidaroid" in nature, but in Clypeaster (Plate 68, fig. 7) and Heteraster (Plate 69, fig. 2) their multiplication is achieved by the introduction of reduced plates. The reason for the introduction of complexity in Clypeaster can hardly be physiological, since related genera (such as those of the Scutellidæ) with even more plates have low, simple primaries only.

In the case of *Heteraster oblongus* (Plate 69, fig. 2) a peculiarly interesting feature of ambulacral development is found. Areas II and IV are petaloid only in the columns (*a* and *b* respectively) that are in a posterior relation; the adjacent columns are more or less obsolete in the "Bothriocidaroid" manner. Roughly twice as many ambulacrals occur on the adapical surface in the petaloid as in the non-petaloid columns. The plates of the former series are, when fully developed, alternately demi-plates and primaries, so that the perradial suture is not affected by the difference in plating on its two sides. In *Spatangus purpureus* (Plate 69, fig. 1) a similar discordance occurs, but it consists in the incorporation of only one additional plate in

each column concerned. (The demi-plate in area V of the specimen figured is apparently fortuitous, and does not represent any numerical irregularity in the plating.) There could hardly be a clearer illustration of the adaptive purpose of plate-complexity than that afforded by Heteraster, but perhaps the most important morphological feature shown is that of the disparity of plating in the columns of one area. In such a form as *Echinocardium cordatum* (Plate 69, fig. 4) it is obvious that the production of new plates proceeds at a different rate at Ocular III from that at the others. But in *Heteraster oblongus* ambulacrals (*i.e.*, podia) are produced with different frequency in two columns which spring from the same ocular plate. Such irregularity is occasionally met with as a teratological feature in the Regular Echinoidea (see Section 2 (d), Echinus), but it is most remarkable to find it adopted as a normal, and clearly satisfactory, condition in this form. Its appearance is presumably to be ascribed to the budding-out of podial vessels from the radial water-canal at different rates on its two sides. Thus it would appear that the character of ambulacral plating is intimately connected with, and indeed determined by, the growth of the water-vascular system. To the activity of budding from the radial canal all other features of ambulacral development are secondary and subsequent.

The condition of ambulacrum III of Heteraster is equally instructive. In a very irregularly triserial way some of the podial pores are petaloid, and others more or less obsolete, or, at least, not specially modified. Those plates which contain petaloid pores are adradially expanded at the expense of the less specialised ambulacrals, and the latter are usually almost (though rarely quite) occluded. It may be suggested that Heteraster shows a stage in Spatangoid evolution in which the branchial function is beginning to leave the anterior petal, but is still partly exercised there. In any case, the resulting structure is remarkably similar to that found in many of the Palæechinidæ (*c.f.*, Plate 61, fig. 9, Maccoya), and it is reasonable to regard it as an expression of reversionary development, in a sense working back from the "Cidaroid" towards the "Bothriocidaroid" condition of plating. A somewhat analogous structure, without accompanying difference in the pore-pairs, occurs in the so-called "*Ananchytes texana*," Cragin (Plate 69, fig. 3).

In the more specialised Spatangidæ, the respiratory function tends to become restricted to the podia of the paired lateral petals, probably owing to the risk of damage incurred by large podia situated anteriorly in a burrowing animal. In most of these types (*e.g.*, Spatangus, Plate 69, fig. 1) the petal of area III becomes morphologically and functionally degenerate; but in a few, such as Heteraster (*vide supra*) and *Echinocardium cordatum* (Plate 69, figs. 4 and 5) it assumes an unwonted secondary complexity. In particular, the intra-fasciolar part of that area in *E. cordatum* shows a degree of complexity unattained by any other post-Palæozoic Echinoid with which I am acquainted, although in its plate-relations and absence of combination it is strangely reminiscent of some "Perischoechinoid" areas (see p. 384). A comparison of Plate 69, fig. 5, with Plate 61, figs. 9, 10, and 11, shows

that area III of *E. cordatum* is practically a structural repetition of the ambulacra of Maccoya and Lovenechinus. According to MacBride, the very numerous podia which emerge through this part of the anterior ambulacrum have a definitely prehensile function, being extruded to the surface of the sand with intent to capture and drag down small organisms, and to keep the vertical tunnel clear of obstructions. The extreme tenuity of the test of *E. cordatum* probably determines the intensity of complication produced by this most interesting secondary development. Morphologically it is comparable with some of the types of secondary adaptation discussed by Dollo (1910). Morphogenetically it is of great importance, as proving that the rate of production of new plates in an ambulacrum may differ in one and the same area according to the stage in ontogeny reached by the individual. In passing, it may be noted that the internal fasciole of *E. cordatum* seems to act as a limit to the production of complex plating in the ambulacra, and that two of the lateral areas (I and V) have demi-plates in the small parts of them included within the fasciole. Other species of the genus have no corresponding complexity, and it seems reasonable to presume that this species should be considered generically distinct, as it is morphologically peculiar.

Phyllodes and hypophyllodes (see Hawkins, 1911) seem invariably to contain some degree of complexity, and the complication is always reminiscent of triad-formation, although no true combination occurs. Normally one in every three of the plates in these regions tends to become occluded, while the other two, in extreme cases (*e.g.*, Catopygus) become demi-plates. I have nothing of importance to add to the conclusions reached in the paper referred to above, on this matter. It may, however, be remarked that the triple series in the phyllodes are in harmony with the normal disposition of plates and pores in the simpler Diademoida (and in the *Holectypoida*), and that they probably represent an original structure; whereas the complexity of petal III in *Echinocardium cordatum* (with no particular numerical sequence in composition), or the alternating demi-plates of the Clypeastrid petal, are as evidently secondary developments. It is regrettable that the true structure of a phyllode is usually very difficult to determine, especially in fossil forms; but such intended structural representations as those given by Clark and Twitchell (1915), and most other authors, for Cassiduloid phyllodes are either imaginary or based upon imperfect observation. In the Spatangidæ, where no true phyllodes exist, the podia nearest to the peristome seem to possess a function akin to that of taste. The plates through which these sensory podia pass are normally lower than the succeeding relatively obsolete plates, but they rarely attain "Cidaroid" proportions.

The posterior ambulacrals of areas I and V which are enclosed within the subanal fasciole of some Spatangidæ always show some approximation to the "Cidaroid" type, but this is more often due to an increase in breadth than to a decrease in height.

In all non-Holectypoid Irregular Echinoidea the ambulacral plates that are not

situated in any of the special regions above described show a more or less complete reversion to the "Bothriocidaroid" character. They become (or rather remain) high, hexagonal, and alternate with the interambulacrals, with superposed pores in each peripodium (when the pores are double); and they differ from the ambulacrals of Bothriocidaris merely in thickness and in the orad position of the peripodia. In many of the Clypeastroida these plates are imperforate, the pores being scattered over the adjoining interambulacra. This anomalous condition is discussed in Section 3 (c), of the second part of this paper. There can hardly be any doubt that these practically functionless ambulacrals are in a morphogenetically gerontic, reversionary phase comparable with that generally ascribed to the sutures of Prionotropis, or the shape of Baculites, among the Cephalopoda. It is interesting to find some structures showing a late stage of obsolescence in types so apparently specialised as the Irregular Echinoidea. But there is at least as much reason to suppose that a Spatangid is degenerate as to consider it progressive.

To summarise the foregoing remarks, it may be stated that three main types of ambulacral complexity occur in the Irregular Echinoidea, although plate-combination is never found. The triserial complication of the phyllodes seems morphogenetically continuous with that of the simpler Diademoid ambulacra. The complexity of the petals of Clypeaster (and of the lateral petals of Heteraster) is clearly a secondary development designed to increase the number of branchial podia. The extreme elaboration of the anterior petal in *Echinocardium cordatum* is as certainly a secondary adaptation to accompany a secondarily acquired prehensile podial function.

Since the *Holectypoida* occupy a systematic position intermediate between the Regular and Irregular Echinoidea, and are probably in many ways phylogenetically annectant, the transition in ambulacral structure between that of the simpler Diademoida and that of the Spatangoida and other Irregular Orders should be traceable, in part at least, in that group. It is the main purpose of the second part of this paper to indicate those features in the Holectypoid ambulacrum which serve to link together, in some measure, the extremely divergent structures that have been contrasted above. There can be no doubt that the Irregular Echinoidea are descended from one or more Regular stocks; and while this does not necessarily imply that their line of descent passed through the *Holectypoida*, the retarded evolution of that Order, and the approximation to the Regular type that it shows in most features, suggest that the morphogenetic phases of ambulacral change may be there represented.

### (f) "*Localised Stages*" *in Ambulacral Structure.*

Detailed study of the adult and developmental characters of the ambulacral areas of many types of the Echinoidea serves to confirm, in a general way, the application of the law of "localised stages," stated and elaborated by Jackson (1899, 1912). But in the interpretation of the effects of the operation of this law, I am often unable

to follow that author, and the present seems a suitable occasion on which to point out the influence and the limitations of the principle as it affects ambulacra.

Every ambulacral plate may be considered to have a life of its own, in many ways independent of that of the organism to which it belongs. It is originated in the placogenous tissue at the orad margin of the ocular plate, and gradually becomes dissociated from its place of inception by the birth of its later brethren. To some degree this movement of the ambulacral is due to the gradual increase in height of the corona, the oculars moving upwards rather than the coronals moving down. But there is in most, if not in all, cases a definite orad progression of the coronal plates under the influence of the pressure exerted by those developed later. The rate of production of new plates may vary in different areas, and at different periods of growth in the same area. JACKSON'S statement that the plates nearest to the peristome are the earliest formed, while those towards the apex are of later development, is as unassailable as the stratigraphical axiom of the order of superposition of sedimentary strata.

In the Palæozoic Echinoidea and Cidaroida, where the ambulacral plates undergo little alteration during their progress, save perhaps in size and ornament, it is reasonable to regard each column as consisting of three regions—an orad portion built of plates formed early in the ontogeny of the urchin, a mid-zone of mature plates, and an apical part made of plates which are formed late in ontogeny, but are morphogenetically young. In the region first-named, the plates will retain recapitulatory simplicity; in the second, they will show the "full-character" for the species; and in the third (apart from features due to acceleration), will again tend towards simplicity. In so far as the determination of "localised stages" is applied to these groups of Echinoids, it proves both accurate and instructive. But an attempt to recognise similar stages in the Diademoida or Irregular Orders encounters considerable difficulties. In the Diademoid ambulacra, as has been shown above, "growth-pressure" of the advancing columns, and "combination" aided by the development of tubercles, react persistently and with cumulative effect on the ambulacral plates throughout their existence. Although the massed, deformed, and sometimes almost destroyed, plates around the peristome in such a type as Heterocentrotus are, from the standpoint of age, the earliest formed in ontogeny, it cannot be imagined that they retain any traces of the primitive simplicity proper to such plates. Though young ontogenetically, they are old morphogenetically, and the vicissitudes through which they have passed have modified them so completely that they have no original features left. In advanced forms, such as the Echinina, some of the ambulacrals are "born" reduced (by morphogenetic acceleration), but this applies only to the new plates of adult individuals. The first post-larval plates are always either "Bothriocidaroid" or "Cidaroid" in character, but in the course of morphogeny these very plates are liable to undergo extreme reduction or complication.

Again, there can be no doubt that the orad ambulacrals of a Spatangid have

retained essentially the proportions and details with which they were first endowed (owing to morphogenetic stagnation). But in a "Cassiduloid" these orad plates are concentrated into complex phyllodes, albeit they were precisely similar to those of the Spatangid at their inception. The low, "Cidaroid" or complex plating of a petal is not so primitive in character as the high, hexagonal plating at the mid-zone, in spite of the "youth" of the plates in the former region. It must in justice be admitted that JACKSON (1912, p. 57) does not cite the Irregular Echinoidea as illustrating his law of "localised stages of development"; but he considers the Diademoida (Centrechinoida) to be bound by it, and by his application of the principle to such types as Hemicidaris and Salenocidaris gives an interpretation of their ambulacral structure with which I am unable to agree.

Concerning the ambulacrum of Hemicidaris, JACKSON says (*loc. cit.*, p. 56) "Passing dorsally [*i.e.*, adapically], we may pass from compound plates into an area of simple plates *which have dropped all attempts at fusion.*" Later, in respect of *Salenocidaris miliaris*, he writes:—"There is a single primary plate ventrally [*i.e.*, adorally], succeeded by one compound plate, which is again succeeded by simple plates throughout the area, *a case of extreme reversion.*" (In both quotations the italics and words in square brackets are mine.) It seems reasonable to ask for the evidence that the simple plates of the Hemicidarid ambulacrum ever made any "attempt at fusion," actually or phyletically, which attempt they have subsequently "dropped." To my mind, JACKSON'S contention in this matter, as in that of Salenocidaris, could be tenable only on the assumption that development into compound plates is an *original* feature of the components—an utterly unwarrantable hypothesis. He himself admits the obvious fact that newly-formed ambulacrals are typically "Cidaroid" in character, and that any degree of complication they may subsequently assume is acquired during their later individual development.

In phylogeny, as in morphogeny, elaboration in the direction of combination or reduction first appears in the oldest plates of the areas (the orad plates), and if this condition does not extend up the area (*i.e.*, adapically) for any considerable distance, the deduction must surely be drawn that, unless the contrary can be proved, a relatively primitive stage of evolution is represented. As phylogenetic specialisation proceeds, elaboration of structure progressively affects the younger ambulacral plates, until in extreme cases it is impressed upon them at their very inception. The single primary on the peristome margin of Salenocidaris is in no way antagonistic to this view. It has retained its relatively primitive simplicity because it has been preserved from crushing by the perignathic process (which is largely based upon it), and has had no reason for combination owing to the absence of large tubercles on its outer surface. The succeeding plates have been jammed against its immovable apicad margin, and support the largest tubercles found in the ambulacrum. Such seems equally to be the interpretation of the orad plates of Heterocentrotus described above.

As a result of the foregoing considerations, and of facts that will appear during

detailed description of the Holectypoid ambulacrum, I am inclined to doubt the applicability of the "law of localized stages" to the separate plates of any but "Perischoechinoid" or Cidaroid forms. Nevertheless, in respect of the composition of compound plates in the Diademoida, the principle seems well established and plainly illustrated. The number of plates in a compound is determined once for all when all plates in the column (or part of a column) have become combined. No subsequent development can detach components from one compound to add them to another; so that, unless the (clearly mistaken) view of A. Agassiz (1874, p. 642) is adopted, and new plates are supposed to be produced elsewhere than at the ocular margin, the number of components in each compound is fixed, however much alteration in size and shape may befall them. Hence, in such a form as Strongylocentrotus, the orad triads, followed in regular apicad sequence by tetrads, pentads and hexads, affords a striking proof of Jackson's law. Heterocentrotus, in which the most numerically elaborate compounds occur at the mid-zone, is in truth a genus showing reversion in its old age. There the latest formed "young" ambulacrals do not attain such complexity of combination as was reached by previously formed plates when they were of that age.

In the Irregular Echinoidea, apart from the inevitable character that the newly formed ambulacrals are morphologically neanic, the great variety of functional adaptation or lack of utility so modifies the plates during their individual "lives" that no morphogenetic regularity can be traced. In the several areas of one Spatangid, plates which have originated synchronously at their respective oculars may show every degree of morphological variety, from an almost "Bothriocidaroid" retardation to the highest degree of complexity. Moreover, in different types of Irregular Echinoids, the first formed plates may either retain their primitive nature (Spatangidæ) or acquire extreme complexity ("Cassiduloida"); while the last formed plates may maintain their primitive characters (area III of Spatangus), or almost at once attain elaborate specialization (area III of *Echinocardium cordatum*). It is the localised function, not a common and fundamental principle, which determines the stage of development of any particular ambulacral plate in the Irregular Echinoidea.

## PART II.—(1) The Structure of the Ambulacra in the Holectypoida.

This small group of the Echinoidea has undergone many taxonomic vicissitudes between the period (early in the last century) when its few known representatives were called "Galerites," and 1889, when Duncan raised it to the rank of an Order. At the present time it is, perhaps, orthodox to consider it a sub-order "Holectypina" of the Gnathostomatous Irregular Echinoids. However, in a long series of papers in the 'Geological Magazine,' and elsewhere, I have persistently followed Duncan in allowing the *Holectypoida* full ordinal rank. This is not the place to discuss the reasons that have induced me, with ever-increasing conviction, to maintain the distinction between the *Holectypoida* and the Clypeastroida; but it may be submitted,

by way of explanation, that these two sections of the "Gnathostomata" are as distinct in structure as the Cidaroida and Diademoida among the Regular forms, and are similarly related in phylogeny. If the latter groups are to be ordinally distinguished, uniformity of classification should apply a similar distinction to the former.

With regard to the internal classification of the Order, the grouping of genera and families here employed is but little modified from that given in a former paper (Hawkins, 1912, *b*), with the incorporation of the alterations suggested in later essays.* For reasons that will appear in the sequel, I have separated the Holectypidæ from the Discoidiidæ. The affinities of this newly erected family are more towards the Pygasteridæ than the true Discoidiidæ—it cannot therefore remain as a sub-family of the latter group, but is hardly to be transferred to the Pygasteridæ. Full separation seems the only alternative. Similarly the Lanieriinæ (see Hawkins, 1913, *b*), which possess a curious combination of the characters of Coenholectypus and Conulus, cannot be safely affiliated with either group, and must be regarded as a distinct family. To counterbalance this new subdivision of the Order, it is proposed to group the considerable number of morphologically and systematically confusing genera that include Pyrina, Pseudopyrina, Conulus, Globator and Echinonëus into one family, to which Amblypygus is provisionally attached. Whatever may be the real or fancied differences between the genera concerned, the ambulacral structure of all of them is so nearly identical that further discussion of this apparently reactionary change is needless here.

For convenience of reference the classification here employed is subjoined, but it must be regarded as tentative, and in some cases admittedly inadequate or unnatural. A revision of the classification must be postponed until the completion of the morphological studies of which the present paper is one.

Order : Holectypoida.

Family I : Pygasteridæ. Lias to Cretaceous.

Sub-family i : Pygasterinæ.

Genus 1 : *Plesiechinus*, Pomel. Type, *Pygaster macrostoma*, Wright.

Genus 2 : *Pygaster*, Agassiz. Type, *Clypeus semisulcatus*, Phillips.

Genus 3 : *Macropygus*, Cotteau. Type, *Pygaster truncatus*, Agassiz.

Sub-family ii : Pileinæ.

Genus 1 : *Pileus*, Desor. Type, *Pygaster pileus*, Agassiz.

Genus 2 : *Anorthopygus*, Cotteau. Type, *Nucleolites orbicularis*, Grateloup.

Family II : Holectypidæ. Lower Jurassic to Upper Cretaceous.

Genus 1 : *Holectypus*, Desor. Type, *Echinites depressus*, Leske.

Genus 2 : *Coenholectypus*, Pomel. Type, *Discoidea macropyga*, Desor.

Genus 3: *Coptodiscus*, Cotteau and Gauthier. Type, *C. noemiæ*, Cotteau and Gauthier.

* For the application of the terms *Pygaster* and *Plesiechinus*, see Hawkins, 1917.

Family III : DISCOIDIIDÆ. Cretaceous.
Genus 1 : *Discoidea*, Agassiz. Type, *D. subuculа*, Leske.
Section, *D. cylindrica*, Lamarck.
Family IV : LANIERIIDÆ. Cretaceous and (?) Eocene.
Genus 1 : *Dischlectypus*, Pomel. Type, *Holectypus meslei*, Gauthier.
Genus 2 : *Lanieria*, Duncan. Type, *Echinoconus lanieri*, Cotteau.
Family V : ECHINONEIDÆ. (?) Upper Jurassic to Recent.
Sub-family i : ECHINONEINÆ.
Genus 1 : *Pyrina* (*sens. lat.*), including *Globator* and *Pseudopyrina*.
Genus 2 : *Echinonëus*, Van Phelsum. Type, *E. cyclostomus*, Leske.
(?) Genus 3 : *Micropetalon*, Agassiz and Clark. Type, *M. purpureum*, Agassiz and Clark.
Sub-family ii : CONULINÆ.
Genus : *Conulus*, Leske. Type, *C. albogalerus*, Leske.
(?) Sub-family iii : AMBLYPYGINÆ.
Genus 1 : *Amblypygus*, Agassiz.
(?) Genus 2 : *Conoclypus*, Agassiz.

## Order : HOLECTYPOIDA.

There are certain ambulacral characters that occur persistently in all members of the *Holectypoida*, affording useful diagnostic features in the Order. These characters may be summarised as follows :—

(*a*) The ambulacra are straight, lanceolate, and narrow, with the greatest width at or near the ambitus. They are usually flush with the level of the surrounding parts of the corona, but may be very faintly inflated. Their ornament is identical in character with that of the interambulacra, but differs in disposition.

(*b*) The ambulacral plates are numerous and low. In Jurassic types, the majority of the ambulacrals are simple primaries (ornamented in triple series); in most Cretaceous and later types reduced plates occur in considerable numbers, often almost throughout the areas. There is always some structural complexity, and this is typically concerned with the production of "triad-grouping." No true compound plates seem to be developed.

(*c*) The pore-fields are narrow, and situated for the most part close to the adradial margins of the areas. The pore-pairs are usually uniserial, but are apt to become triserial near the peristome (particularly in Conulus), and in a few cases may be regularly biserial (Pileus), or irregularly multiserial (*Discoidea cylindrica*) in other parts of the areas. In Jurassic forms the pores of the adapical surface are usually somewhat larger than those of the adoral surface—these proportions are typically reversed in Cretaceous and later groups. In the former case, especially in the Pygasterinæ, a feebly sub-petaloid tendency is found; but the disparity of the pores of a pair is always slight, and there are no defined limits to the region in

which it occurs. In the Amblypyginæ, a definitely petaloid quality is developed. There is a fairly constant reduction in the average size of the pores from Jurassic to Cretaceous times, but the pores are always paired, and almost always enclosed in peripodia.

It is worthy of comment that in this three-fold analysis of the Holectypoid ambulacrum, the majority of the features prove to be essentially identical with those of the simpler Diademoida. In three details only is any marked difference found; (*a*) the ambulacra are relatively narrower than is usual in the Diademoida (although in some cases, *e.g.*, Salenia and Heterocidaris, much narrower areas occur than in any of the *Holectypoida*), (*b*) the ambulacral plates are never combined (though always partially grouped into triads), and (*c*) the pores may be slightly dissimilar, or else exceptionally minute. These three points of difference are overshadowed by the many features of similarity; indeed, the first two are more apparent than real, and might almost be cited as *resemblances* to the more primitive Diademoid ambulacra.

## Family I: Pygasteridæ.

The general characteristics of the Pygasterid ambulacrum may be summarized as follows:—

(*a*) The ambulacra are symmetrically lanceolate and, though narrow, are proportionately wider than in the adults of other families. The perradial tracts are commonly inflated, but to a small degree only. The tubercles of the adapical surface are small and widely spaced, those of the adoral surface larger (particularly in respect of their scrobicules), while near the ambitus they are congested in such a manner as to become polygonal. Their arrangement is very regular, consisting of repetition on every third plate.

(*b*) The ambulacral plates are low, simple primaries over the entire adapical surface; although they become distorted in the region of crowded tubercles, and often become grouped towards the peristome, they retain their primary character with very rare exceptions over the adoral surface. When grouping of the plates occurs, the triad principle is always adopted. The plates tend to increase in height from the ambitus to the peristome, whether grouping affects them or not.

(*c*) The pore-fields are narrow, often slightly sunken adapically. The pores of each pair are separated by a very narrow space (occupied by a granular excrescence), and the outer pore is usually very near to the adradial suture, if not actually in contact with it. Adapically the pore-pairs are in very close uniserial sequence (except in Pileus); they become even more congested at the ambitus, without departing from the uniserial order; adorally they are more widely separated, and may show obscure triserial arrangement (well marked in Pileus). In most genera the pores are slightly dissimilar on the adapical surface, the outer pore being elliptical or ovoid in shape, while the inner pore is circular or crescentic. In all cases the apical pores are

distinctly larger than those at the ambitus or on the adoral surface. All the pore-pairs are enclosed in peripodia, but these are well-defined only on the adoral surface.

## Sub-family i: PYGASTERINÆ.

There are no ambulacral characters of a general nature in this sub-family which need be added to those given above.

### Genus 1: *Plesiechinus*, Plate 65, figs. 1 and 2.

The type of this genus, *P. macrostoma* (Wright) is rare and not well known. Thanks to Mr. L. RICHARDSON, I have been able to make a sufficient study of the ambulacra of two specimens to determine that their structure is essentially identical with that in *P. ornatus* (BUCKMAN). The specific distinction between the two forms is but slight, and the justification for the retention of *P. macrostoma* as a distinct species rests more on stratigraphical than on morphological evidence. *P. ornatus* (usually miscalled "*Pygaster semisulcatus*"), which occurs at a considerably lower horizon (*η murchisonæ*), is, like most abundant forms, exceedingly variable in shape and ornament. One variety only (*P. conoideus*) has been named, but there are at least six others in my collection that are equally worthy of separation. However, none of the differences in shape, ambital angle, or ornament seem to be associated with any important modifications of ambulacral structure, so that the following description holds good for all forms of this protean species and, I believe, is essentially true for the genus:—

(*α*) The Ambulacra.—Areas II, III, and IV are straight, and of almost exactly the same length. Areas I and V are more or less curved adapically owing to the great width of the periproct and the wide separation of the posterior oculars. They are also slightly shorter than the others, since the apical system is a little excentric posteriorly. The areas are all regularly lanceolate, but except in the apicad and orad quarters, their adradial margins are very nearly parallel. The inflation of the perradial tract is well marked in some varieties, faint in others, but is always present and never considerable.

The ornament is dense, like that of the interambulacra, consisting of primary and secondary tubercles, and variously sized granules. In young forms the tubercles occur in single rows down each column, placed nearer to the pore-fields than to the perradius, and situated on every third plate. In older examples a second, inner row of tubercles appears, placed nearer to the perradius than the earlier series, and situated on the plates immediately adoral to the originally tuberculate ones. This tubercle series never seems to extend more than half the distance from the ambitus to the apex or peristome. In fully developed specimens a third perradiad row occurs in the immediate vicinity of the ambitus. It is usually rather sporadic, and its tubercles rarely attain the dimensions of those of the other rows; very commonly

they are developed in one column only. These tubercles are usually situated on the plates that do not support members of the other two series, but they are rather irregular in distribution, and may sometimes be developed on the plates bearing tubercles of the first series. On the adapical surface the tubercles are relatively small, but their shallow scrobicules always extend across the apicad transverse sutures of the supporting plates, and not infrequently encroach slightly upon the contiguous orad plate. On the adoral surface the tubercles increase in height, but the bosses are not much greater in diameter than above. The scrobicules, however, become much wider and more deeply excavate; often they meet one another, and are then separated by a low, smooth ridge. Towards the peristome, where tubercles of the first series alone persist, the scrobicules become disproportionately large and take on an elliptical shape with the longer axis longitudinal; the bosses rise abruptly from the scrobicules, and are placed near the orad foci.

(*b*) The Ambulacral Plates.—From the ocular margin to a point slightly below the ambitus, the plates are simple primaries, alternating regularly in the two columns. Though constantly low, they diminish steadily in height in the direction named, becoming lath-like, with somewhat distorted transverse margins, in the region where the tubercles are most densely congregated. This condition extends to a point at rather less than one-quarter of the distance from the ambitus to the peristome. In the remaining three-quarters of the adoral parts of the areas, the plates increase rapidly in height, though undergoing a fresh diminution quite near the peristome. They are, on the average, twice as high in this region as on the adapical surface. Corresponding with this change in proportions comes a departure from simplicity. A fairly regular (though rarely perfect) grouping takes place, in such a manner that the transverse sutures meet the perradial line in groups of three. This result is attained largely by the perradiad lowering of the plates apicad to those bearing the tubercles of the first series. These plates may occasionally become demi-plates, but they are rarely much separated from the perradial suture. It is worthy of note that such demi-plates are more frequent, and better defined, in areas I and V (the short ambulacra) than in the others. A careful study of the grouping of the plates in this region shows that there are really two separate zones. One exists in that (apicad) portion where the second tubercle series occurs, the other (orad) where there are only the main tubercles. In the former zone, the plates which support the perradiad (second-series) tubercles are perradially expanded, while the other two, though both primaries, are low. In the latter, the plates bearing the tubercles of the first series are expanded, while the other two remain low, or may even be reduced. The meeting of these two discordant grouping-systems is usually marked by the presence of one or more pairs of normally alternating primaries (see X in Plate 65, fig. 2).*

* A similar drawing of the adoral part of the ambulacrum of *P. ornatus* is given by LOVÉN (1888). My figure was drawn quite independently of his, and the close correspondence between the two shows how constant are the ambulacral characters in this species.

That the distortion of the plates in the former zone is due to the presence of the perradiad series of tubercles can hardly be doubted, but it is noteworthy that distortion is the only feature there; there is no reduction. In the latter zone the plate-grouping seems to have a more fundamental origin. Although the expanded plates are again those that support large tubercles, it is clear that the reduction of other plates is quite unnecessary for the accommodation of these tubercles. Indeed, the reduction does not become appreciable until the transverse suture affected has passed or even crossed the boss. Again, tubercles with scrobicules transgressing the sutures even more widely occur on the adapical surface, with no accompanying disturbance of the plating. In this orad region of plate-grouping we have an almost perfect repetition of the alternate dyads and simple plates found in Acrosalenia (Plate 62, fig. 4), with the sole difference that no true combination occurs in *P. ornatus*. The fact, noted above, that demi-plates are most marked in this region in areas I and V (where the actual number of plates in these shorter areas is the same as that in the others) suggests that the plate-reduction (and grouping) is due to "growth-pressure" rather than to any direct influence of the tubercles. On the other hand, the relatively great height of the plates seems inconsistent with compression in the ordinary sense. The grouping extends into the peristomial invagination, and usually only one pair (rarely two) of normally alternating primaries occurs on the margin.

There is reason to believe that the proximal peristomial ambulacrals are really the first coronals of the areas. There are traces of slight marginal resorption, and probably the extension of the branchial incisions has modified the plates adradially. But since the primordial single interambulacral plate is constantly preserved, and the ambulacra project into the peristome at least as far as the interambulacra, it seems probable that no actual destruction of plates has occurred. This argument holds good for the whole Order.

(*c*) The Pore-fields.—The pore-pairs are perfectly uniserial, from the apex to the region where true plate-complexity begins. Over the inner half of the adoral surface they become progressively triserial towards the peristome. The pairs situated on the non-tuberculate "monads" are shifted in a perradiad direction (though but slightly), while those of the other two pairs retain their adradiad positions. Thus the disposition of the pore-pairs is not typically triserial, but might be described as showing an interrupted uniserial sequence, with every third pair out of the straight line. This condition, though apparently trivial, distinguishes the orad parts of the pore-fields of Plesiechinus from those of Acrosalenia and other Diademoida, and makes them comparable with the phyllodes of the Nucleolitoida and Cassiduloida. It is perhaps legitimate to describe this part of the Plesiechinid ambulacrum as an incipient phyllode, not worthy of the name *hypophyllode* (see Hawkins, 1911, p. 260), but none the less suggestive of the quality so named. The pores of the adapical surface are usually faintly dissimilar, the inner one being

circular or gibbous, the outer one slightly elliptical. No condition that could be termed *sub-petaloid* is attained, but the character of the pores is suggestive of incipient petaloid structure, much in the same way that their disposition adorally is pre-phyllodal. There is little change in the size of the pores throughout the length of the areas, but they are always similar ambitally and adorally. In the latter region they may diminish in size in some cases, and the pore-pairs always become widely spaced, in contrast with their crowded disposition elsewhere. Roughly, two-thirds of the pore-pairs are situated above the ambitus:—the average figures (taken from all five areas, in 25 specimens of varying size) being 63·1 per cent. adapical, 36·9 per cent. adoral. Since the corresponding lengths of the areas average 58·5 and 41·5 respectively, there is a real excess of podia on the adapical surface. Moreover, the zone of ambital crowding extends for a short distance on to the adoral surface, and this tends to obscure the very considerable disparity in numbers and spacing of the pores on the two surfaces of the test. It is of interest to recall in this connection that the tendency in Diademoid ambulacra is to produce congestion near the peristome, while that in the Irregular Echinoids (especially in the Spatangidæ) is to reduce the adorally situated podia both in numbers and function. Plesiechinus undoubtedly conforms more to the latter condition, though retaining ambulacral structure which is essentially similar to that of the early Diademoida.

(*d*) Abnormalities.—In the very numerous examples of *P. ornatus* that I have examined, only one case of abnormality has been noticed. This is exactly identical with the malformation shown in *Pygaster macrocyphus* (Plate 65, fig. 6), and its description may be postponed until that species is considered. Trifling irregularities in the proportions of the ambulacral plates are frequent, but those that have been observed never obscured or interrupted the normal plating structure. In one specimen, the operations of a boring parasite have caused the secretion of a kind of callus over the outer surface of the test in the part affected, and, although this has involved the obliteration of two contiguous pore-pairs, it is not a development that demands consideration in the present enquiry.

Genus 2: *Pygaster*, Agassiz, Plate 65, figs. 3, 4 and 6.

This typically Upper Jurassic genus, which attains its fullest development in the Corallian, is in great need of systematic revision. The type, *P. semisulcatus* (Phillips), (long miscalled "*P. umbrella*"), is the only Corallian species recognized by name from Britain, but there are at least two others from that horizon that are relatively abundant, especially in the South of England. Numerous examples of these three forms (chiefly in the Oxford Museum), and the co-type of *P. macrocyphus* (Wright), from Boulogne, have afforded the evidence from which the ambulacral characters of the genus have been deduced. They all agree in essentials, and, for the sake of uniformity, the actual description has been drawn up from a fine specimen of the genotype (from the typical locality, Malton) now in the

collection of the Geological Department, University College, Reading, No. 804. This specimen is very closely similar in size, form and ornament to the lectotype in the British Museum (see HAWKINS, 1917), and, in so far as can be determined, agrees absolutely with it in ambulacral structure. The latter specimen cannot, for obvious reasons, be maltreated by the staining and other preparatory processes to which the former has been subjected.

(*a*) The Ambulacra.—The areas differ from those of Plesiechinus in two respects only. They are relatively wider (to a small degree only) at the ambitus, and, indeed, over most of the adapical surface; and they taper towards the peristome through their whole adoral extent, instead of retaining almost the full width for some distance below the ambitus. Their ornament is different in detail, though similar in general nature and distribution. On the adapical surface the tubercles are relatively small; they increase rapidly in size at the ambitus, and become disproportionately large towards the peristome. There the scrobicules are very wide, practically circular, with small, central bosses, quite unlike the elliptical areolæ of Plesiechinus with their excentric tubercles. In the neighbourhood of the ambitus, the second series of tubercles attains dimensions fully as great as those of the first series, so that, although a third series is only very feebly developed, there is far more congestion of the tubercles than in Plesiechinus, and most of the scrobicules are sharply polygonal in outline.

(*b*) The Ambulacral plates, Plate 65, figs. 3 and 4.—On the adapical surface the ambulacrals in Pygaster are similar in proportions and characters to those similarly situated in Plesiechinus. Towards the ambitus they become even lower than in the latter genus, and their transverse sutures tend to be sinuous. Just below the ambitus somewhat irregular triad-grouping appears, clearly due to the presence of perradiad tubercles. This superficial dislocation of the transverse sutures is closely analogous with that found in Plesiechinus, but it comes on considerably further from the peristome than in that genus. It persists for about half the length of the adoral part of the area, but its orad limit is again further from the peristome than in Plesiechinus. This difference in plating is to be correlated directly with the difference of tuberculation between the two genera. In the parts of the ambulacra between the orad end of the dislocated plates and the peristome a surprising contrast from the Plesiechinid condition is found. Although the main tubercles are larger in Pygaster, the plate-structure is almost perfectly simple. Occasionally an imperfection of alternation of the columns occurs, but there is no suggestion of a triad-grouping of the plates—they are all primaries, and usually simple ones. The ambulacra of Pygaster have lost all traces of Diademoid structure, although their ornament still retains the primitive ternary arrangement. This regressive simplification constitutes, to my mind, one of the most definite diagnostic characters of the genus, and of itself would be sufficient to warrant the recognition of generic distinction between Pygaster and Plesiechinus. Since almost

all Jurassic Irregular Echinoids retain some traces of triad-arrangement near the peristome, Pygaster proves, in this respect, to be more advanced towards the Spatangid character than any of its contemporaries—a somewhat unexpected condition.

(*c*) The Pore-fields.—The pore-pairs are uniserial almost throughout. Quite near the peristome a faint tendency to triserial arrangement occurs, but it is not so pronounced as in Plesiechinus. The pores of the adapical surface are markedly dissimilar, particularly towards the apical system. The outer pores are elliptical, and the inner usually quite circular. Although it would hardly be correct to describe the pore-fields as sub-petaloid, the tendency towards that condition is considerably greater than in Plesiechinus, while the restriction of dissimilarity to a part of the adapical surface only serves to emphasise the suggestion of an incipient petal. In *P. macrocyphus* (Plate 65, fig. 6), from the Kimmeridgian, it is hardly possible to avoid the term sub-petaloid in a description of the pore-fields. Certainly, such a designation is more appropriate in that case than when applied to Galeropygus, and many even of the later Nucleolitidæ. The pores of the adapical surface in Pygaster are considerably larger than those of the adoral region, and show a progressive diminution in size when traced from the apex to the peristome. They are much smaller adorally than in Plesiechinus, and are not so widely spaced. There is a similar ambital congestion in both genera. In the specimen of *P. semisulcatus*, on which the foregoing description is chiefly based, 55·4 per cent. of the pore-pairs are on the adapical, and 44·6 per cent. on the adoral, surfaces respectively. Closely similar percentages have been calculated in several species of the genus. It is somewhat surprising to find a greater approximation to evenness of distribution of the podia in Pygaster than in Plesiechinus, especially since the ambulacral structure in the latter genus is more "Diademoid" than in the former.

(*d*) Abnormalities.—The number of specimens belonging to this genus that have been studied is far inferior to that in the majority of genera here described; and, perhaps as a consequence of this, no abnormalities of any kind have been observed save in one specimen, the cotype of *P. macrocyphus* (Plate 65, fig. 6). In that case, area II shows a particularly good example of an irregularity of development that is not at all uncommon in the *Holectypoida* and Cassiduloida. The present seems a suitable occasion for giving a description of this abnormality, although it seems to be of a kind that involves few morphogenetic points of interest. In the specimen here figured, at a point almost midway between the ocular and the ambitus, area II becomes rapidly narrowed for about six plates, and in the next six recovers its full width. At the narrowest point the area has only about half the width proper to the region. Both columns are affected alike, and the plates of both become cuneiform (narrowing adradially) where the constriction is most complete. At the region of maximum constriction there is an exceptionally large tubercle situated exactly over the perradial line. No traces of sutures can be detected on the boss;

and, in other cases, none can be found by methods that expose all the surrounding sutures clearly. One or two structurally single plates reach right across the area, bearing pore-pairs at both (adradial) ends. There can be little doubt that originally the perradial suture was continuous, and that the two columns have been subsequently united by anchylosis or syzygy. The cause of this type of abnormality is obscure. It may occur at any point in the length of an area, and, in a specimen of *Holectypus hemisphæricus* that I have examined, it occurs twice in one area, on the adapical surface and just below the ambitus. Since all the ambulacrals are narrow at their inception, it might result from the failure of some of them to widen during growth, but the presence of the central tubercle, and the symmetrical constriction of both columns, seem to indicate that the irregularity is inborn in the plates. There is never any sign of accidental fracture, or of corresponding imperfections in other parts of the corona. In one case (of *Holectypus hemisphæricus*) the constriction occurs in two areas (I and V) at the same horizon just below the ambitus, but in all other observed cases it affects one area only. As noted above, I have seen it in one specimen of *Plesiechinus ornatus* and one of *Pygaster macrocyphus*. It occurs in fifteen out of some hundreds of specimens of *Holectypus hemisphæricus*, and in one out of several score of *H. depressus*. I have not found it in Discoidea or Conulus, in spite of the great quantities of material representing those two genera that have passed through my hands. It has been noticed in two cases in *Galeropygus agariciformis*, one of *Hyboclypus gibberulus*, two of *Nucleolites scutatus*, and one of *Clypeus sinuatus*. In all these cases the structure is identical with that described above, and must surely be ascribed to the same cause, whatever that may be. A constriction, similar save in the absence of the median tubercle, affects part of the petal of area II in a specimen of Echinolampas from the (?) Miocene of Persia, recently sent me by Mr. H. Woods. I have not found any comparable abnormality in any of the Spatangoida. It is regrettable that no clue to its origin and meaning is as yet forthcoming.

### Genus 3: *Macropygus*.

I have been unable to obtain sufficient material for the study of the ambulacra of *M. truncatus*, which has not been found in Britain. From the few specimens seen, and reference to published figures, it would appear that the structure of the areas is very nearly the same as that in Pygaster. There is no indication of triad grouping adorally, nor do the pore-pairs depart seriously from a uniserial sequence. In one respect there is a marked difference from Pygaster, and even from Plesiechinus. The pores are minute throughout, with little or no dissimilarity on the adapical surface. The tentative efforts at petaloid structure that are characteristic of nearly all the Jurassic *Holectypoida* seem to have been abandoned in this, as in other Cretaceous genera in the order.

### Sub-family ii : Pileinæ.

The two genera here associated in this sub-family are so grouped for convenience. It is more than doubtful that any close relationship links Pileus with Anorthopygus. The position of the periproct is almost the only feature of importance that they have in common ; and any lines of descent from a Pygasterine origin towards the truly Irregular type must needs have passed through such a phase. Anorthopygus is very possibly a descendant of Macropygus while, on stratigraphical evidence, Pileus must have some other ancestry. Neither of the genera has been studied under satisfactory conditions. Pileus is not known from the British Corallian ; while Anorthopygus, though represented in the British Cretaceous fauna, has been found only in the Haldon Hill remanié and the Hibernian Greensand, and specimens showing details of the surface of the test have yet to be discovered. I am, therefore, unable to add to the exiguous accounts of the ambulacra of the two genera that have been published.

#### Genus 1 : *Pileus.*

This rare and large form is unique in the order in having the pore-pairs arranged biserially throughout the adapical parts of the ambulacra. The zig-zag series of pores resemble those of Diplocidaris or Diplopodia. They agree with the pore-pairs of Diplocidaris in the homogeneity of the pores, and their large, elliptical shape. But their peculiar disposition is not associated with any diversity of plate structure, so that in that respect they are more like those of Diplopodia. It is an interesting and suggestive coincidence that the appearance of the biserial adapical pores of Pileus should occur in the Corallian, during which period the comparable development in Diplopodia arose. Whether the development is adaptive to some special circumstances incidental to life on a coral-reef, or is a case of (somewhat remote) synchronous parallelism, cannot well be determined. The "diplopodous" condition of the apicad pores in Heterocentrotus and Colobocentrotus lends some support to the former alternative, although many of the Cretaceous Diplopodiidæ were certainly not reef-dwellers. On the adoral surface the pores of Pileus are quite minute, and not biserial, but they remain somewhat congested throughout. They are triserial over a large part of this surface, the triplets becoming progressively more oblique as they approach the peristome. De Loriol (1890, p. 116) describes the pore-pairs as "grouped in little arcs of three or four pairs." Quadriserial arrangement would probably be a local and individual irregularity. The whole of the adoral surface is densely covered with tubercles (as many as four series of tubercles occurring on each ambulacral column at the ambitus), and that feature, coupled with the triserial arrangement of the pore-pairs, suggests that some plate-complexity may occur (either intrinsic or tubercle grouping), but no descriptions or drawings give any evidence on this point.

### Genus 2 : *Anorthopygus*.

This Cenomanian genus has thickly tuberculate ambulacra, like Pileus, but no other resemblance occurs in the areas. The pores are minute and practically uniserial throughout, closely resembling those of Macropygus. LAMBERT (1911, p. 74) states that in *A. michelini* "the ambulacrum is entirely composed of primaries," but does not indicate whether any irregularity of alternation occurs between the columns. On a flint mould of *A. orbicularis* from Haldon the indications point to a perfectly "Cidaroid" disposition of the plates throughout, but it is unsafe to rely upon the somewhat obscure evidence afforded by it, especially since sutural irregularity due to tubercle growth is often far less marked within the test than on its outer surface. Nevertheless, all available evidence suggests that in Anorthopygus the simplification of plating initiated by Pygaster has been carried to its conclusion. According to COTTEAU (1859, p. 178) the pore-pairs become "a little oblique" near the peristome, but they may have a like disposition in Pygaster without any accompaniment of disturbance in the plating.

### Family II : HOLECTYPIDÆ.

In spite of the diversity in structure and ornament of the three genera at present constituting this family, the ambulacral characters are remarkably constant. Even the important advance marked by the redevelopment of the posterior gonad in Coenholectypus is unaccompanied by any morphogenetic acceleration in the ambulacra. Since the only appreciable departure from the usual plating character occurs in a species usually identified with the genotype of Holectypus, it will suffice here to indicate the structure normal to the family without detailed reference to the several genera. In *Holectypus hemisphæricus* (Plate 65, fig. 8), one of the earliest species of the family and one attaining an average size, the ambulacra differ from those of the almost contemporaneous Plesiechinus only in dimensions and the absence of subpetaloid tendencies. Occasional demi-plates may occur in the region of "Acrosaleniid" plating, and the complication near the ambitus due to tubercle crowding is usually less marked than in the larger genus. There is a considerable range of variation in the number of grouped triads present, some specimens having only two such groups in each column, while others of the same size may have as many as six. It is perhaps worthy of note that when the amount of grouping is small, the degree of reduction of the plates is more intense. In the distribution of the pore-pairs (*i.e.*, plates) on the corona, *H. hemisphæricus* shows a fair correspondence with *P. ornatus*. Fifty-six specimens of almost the same dimensions from one locality (Burton Bradstock, Dorset), and from the same hemera (*schlœnbachi*) gave an average of 34·2 per cent. of pores on the adoral surface, as compared with 36·9 per cent. similarly situated in Plesiechinus. It should be noted, however, that this average figure is deduced from a series in

which the extremes are so far separated as 28·3 and 39·4 per cent. Perhaps a biometric study of this character in larger numbers of specimens might show the existence of more than one lineage.

The small *H. depressus* from the Inferior Oolite (presumably the type of the genus) is essentially similar to the species described above, as regards ambulacral structure, but there is a tendency for the plates of the adoral surface to be rather higher near the peristome. As a result, the pore-pairs of that region are widely spaced, but a compensating congestion occurs near the ambitus, so that the average percentage of plates on the adoral surface remains about the same. All other species of Holectypus and Coenholectypus that I have been able to study, except the one about to be described, are remarkably constant in the resemblance of their ambulacral structures to those of *H. hemisphæricus*.

The common species from the Cornbrash, which is usually called *H. depressus*, is superficially remarkable for the great size that it may attain. Specimens with a diameter of about 50 mm. are frequently met with, while the Inferior Oolite species rarely exceeds half those dimensions. The form is probably that named *H. striatus* by D'ORBIGNY, but since a systematic discussion would be out of place here, I prefer to call it *H.* "*depressus*" without prejudice to later specific determinations. A casual inspection of the ambulacra of this form shows that there is a great number of very low plates, with crowded pore-pairs, on the adapical surface, and a strange paucity of them, with widely spaced, somewhat large pore-pairs, adorally. The crowded primaries pass round and a little below the ambitus, but give place to high, almost "Bothriocidaroid" plates at the point where grouping begins. Plate 65, fig. 7, indicates this feature in an average specimen, while Plate 65, fig. 9, shows a somewhat extreme case. The plating-structure of the complicated region is seen to be essentially like that of *H. hemisphæricus* or Plesiechinus, but the proportions of the plates are extremely different. The average percentage of plates and pores on the adoral surface (calculated from all five areas in 12 specimens) is 24 per cent., but even this low figure does not adequately express the condition, since a considerable part of the area just adoral to the ambitus is occupied by crowded primaries. Only among such specialized Echinoids as *Clypeus sinuatus* or the simpler Spatangidæ can a similar distribution of the ambulacrals be found. But *C. sinuatus* has highly developed petals, whereas there is very little disparity in the apicad pores of *H.* "*depressus*." It is doubtful whether this transference of the podia to the adapical surface (without any demonstrable change in their function) has any phylogenetic significance, but morphogenetically it seems explicable as a precipitate, but incomplete, progress in the direction followed more gradually by most Irregular Echinoids, and towards the goal that has been reached by the most advanced Spatangoida.

## Family III : Discoidiidæ.

Although this family includes but a single genus (according to present systematic grouping), the ambulacral structure developed within its limits is more diverse, and in many respects more elaborate, than that of any other family in the Order. For those reasons detailed description is necessary; while the undoubted phyletic affinity between the family and the Clypeastroids lends an unusual interest to its morphological peculiarities. In a general way, the genus Discoidea may be divided into two sections, comprising small and large species respectively. Pomel (1883) distinguished the latter section by the name Pithodia, but later authors have rarely, if ever, accepted this genus. I am convinced that some such separation of the two groups is both convenient and natural, but, to avoid systematic discussion, I prefer here to refer to the two sections as *Discoidea cylindrica* and "the other Discoidiidæ." The latter group includes *D. subucula*, the genotype, and, as far as my experience goes, all other species save *D. cylindrica*. Unfortunately, the small forms that conform to the type in essentials are extremely difficult to examine. This difficulty is partly due to their small size, but it is exaggerated by the extraordinarily thick granulation of their tests. Staining is an almost inevitable preliminary to the tracing of sutures, especially in small forms, and the linear arrangement of the minor ornament causes innumerable spurious suture-lines to appear under such circumstances. Out of several hundreds of specimens of *D. subucula* I have only one example in which (in one area only) it is possible with certainty to trace the sutures throughout the ambulacrum, and a similarly unique test of *D. dixoni* has been selected from 75 specimens. It has, however, been possible in the case of both species to detect the sutures here and there, and on every such occasion the structure has proved very nearly identical with the corresponding sections of the complete areas. In no other species of this group have I been able to trace the ambulacral sutures, and it is only on the evidence supplied by the disposition of the pore-pairs that I have concluded that such forms as *D. favrina* and *D. decorata* are akin to *D. subucula* rather than to *D. cylindrica*.

### Species 1 : *D. subucula* (Plate 67, fig. 1).

(*a*) The Ambulacra.—The areas of this small species are very regularly lanceolate in outline, conforming in this respect, as in many others, to the Jurassic rather than to the Cretaceous quality. Small forms are often retarded in morphogeny, and, considered alone, *D. subucula* affords a striking illustration of that principle. The ornament is disposed in much the same manner as that of Holectypus, but tubercle-series additional to the main one are usually sporadic.

(*b*) The Ambulacral Plates.—Reference to the figure will show how closely in accord with the plating of the Jurassic Holectypoida is that of *D. subucula*. Adorally the plates are grouped into triads, as in Plesiechinus, but the grouping

extends further from the peristome in the small Cretaceous species, since none of it seems to be due to tubercle-growth. In this respect alone is any advance apparent. Although some of the reduced plates are almost separated from the perradial suture, I have never seen a definite demi-plate in this species. At the ambitus, and for some way up the adapical surface, the plates are low, crowded primaries resembling those of Holectypus, but over the apicad half of that region they become relatively high. Were the species to be considered alone, this marked feature of the apicad ambulacrals might reasonably be regarded as a retention of morphoneanic characters due to the small size of the corona, but the description of *D. dixoni* which follows shows that it is an expression of some more important tendency.

(*c*) The Pore-fields.—The podial pores are uniformly minute, and seem perfectly homogeneous. Near the peristome they tend to depart from a uniserial sequence, but there is no definite triserial arrangement. In the specimen figured, 42·6 per cent. of the pores are on the adoral surface, and this seems to be approximately their average distribution. Such a percentage is quite out of keeping with those in Holectypus, or even in Plesiechinus, but is similar to that in Pygaster. It shows a tendency towards an equalisation of the distribution of the podia that points in a direction definitely away from the Spatangidæ. It is, however, more reasonable to consider the area as consisting of three parts—an adapical region of few pores, an ambital region of crowded pores, and an adoral region of less crowded, but still close pore-series situated in a zone of complex plates.

Species 2 : *D. dixoni* (Plate 67, fig. 2).

This small species which is sometimes identified with *D. minima*, is abundant in the lower part of the Middle-Chalk zone of *R. cuvieri*. In size, ornament and general characters it is very similar to *D. subucula*, almost the only superficial distinction being the relative inflation of the ambitus. It is therefore reasonable to suppose that *D. dixoni* is a late development from the *D. subucula* stock, and that it should show the trend of morphogenetic evolution therein. That the latter supposition is justified is clear from a comparison of Plate 67, figs. 1 and 2. The specimen of *D. dixoni* from which fig. 2 is taken, has practically the same diameter as the *D. subucula* analysed in fig. 1. The two figures are thus similarly enlarged, and show comparative features of unexpected interest. The more obvious difference between the two ambulacra may be expressed by the number of plates in the columns. While in column *a* of *D. subucula* there were 75 plates, in that of *D. dixoni* there are only 46. The inflation of the supra-ambital parts of the test in the latter species probably accounts for the low percentage (39·1) of plates on the adoral surface.

Throughout the area the plates are much higher than in *D. subucula*, and there is but a faint tendency to ambital congestion. But while the plates are fewer and more primitive in proportionate height, the amount and degree of complexity is much

greater in the later species—*D. dixoni*. Grouped plates extend from the peristome to a region well above the ambitus, and much-reduced demi-plates are the rule rather than the exception. Indeed, the adoral part of the ambulacrum is extraordinarily like the greater part of the area in Conulus (fig. 3), and even more like that of a young Echinonëus (fig. 5). The apicad plates, on the other hand, are not only primaries, but are almost "Bothriocidaroid" in character, showing a considerable progress along the line of simplification indicated in *D. subucula*. The ambulacrum of *D. dixoni* thus exhibits two apparently opposite qualities, an advance in complication and a regression in plate-production and form. Such a combination of structures seems explicable as a tendency towards the Fibulariid character (see below, Section 3 (*c*)), and the adoral part of the area certainly suggests affinity or parallelism with the Echinonëid ambulacrum.

Section : *Discoidea cylindrica* (Plate 66).

This large and well-known species has a considerable range (approximately coinciding with the Cenomanian), and appears to have two distinct forms. Specimens from the Upper Greensand are usually relatively small, and almost always have markedly cylindrical tests. In the Chalk Marl depressed or hemispherical forms are perhaps more abundant, but large specimens from that horizon are usually cylindrical. In the zone of *H. subglobosus* cylindrical tests, often attaining a very large size, are normal for the South of England, while the depressed type, commonly of relatively small diameter, seems more characteristic in Lincolnshire. Opinion is divided as to whether the "*forma vulgaris*" (Lovén) and the "*forma depressa*" are distinct species. It has been claimed that differences occur in the structure of the perignathic girdle, but I believe that these are not constant. The alternative view that the cylindrical forms are gerontic is somewhat discounted by the prevalence of small cylindrical specimens in the Upper Greensand, and by the occurrence of depressed tests of greater diameter than some that are cylindrical at higher horizons. Except for inevitable difference in the percentages of plates on the two surfaces of the test, I have been able to find no definite differences in the ambulacral characters in the two forms, and hence associate them under the same name for the purpose of the present paper.

(*a*) The Ambulacra (Plate 66, figs. 1, 4, 5, and 6).—The outlines of the ambulacra show a distinct, and in some measure a progressive, departure from the lanceolate type. The greatest breadth is usually a little above the ambitus, and is attained (from the ocular margin) by a very regular increase. From the region where the adoral surface becomes flat a rapid diminution in width sets in, and the areas taper with straight margins to the peristome. In cylindrical forms there is a tendency for the part just above the ambitus to be locally widened (fig. 4), while in depressed specimens the sides of the areas are either parallel or even concave in that region (figs. 1, 5, and 6). Ornamentation (Plate 66, figs. 2 and 3) is sparse except at the

ambitus, but there it becomes exceedingly dense both on the ambulacra and inter-ambulacra. In no observed cases do the tubercles transgress the transverse sutures, and their "triserial" arrangement is often imperfect, although always recognisable. Adorally the tubercles tend to occur on every alternate primary, as in Echinus. Towards the peristome a line of prominent granules occurs down each column between the pore-fields and the adradial sutures (fig. 3), one granule rising from each plate with great regularity. It is clear that the ornament, from its small scale and frequent lapse, cannot be held responsible for the intensity of the plate-complexity.

(*b*) The Ambulacral Plates.—Complexity in a degree unknown in other Holectypoida, and, indeed, in other Irregular Echinoidea, charaterises the plating of the ambulacra over their whole adoral extent, and affects the plates for a variable, but always considerable, distance above the ambitus. The original of Plate 66, fig. 1 (in the Manchester Museum), is a large specimen, with a diameter of 57 mm., and, though merely labelled "Lower Chalk," was almost certainly collected from the *H. subglobosus* zone. Adorally a few primaries persist, but even these are more or less grouped. Then follow two triad-groups (similar to those of the adoral surface of *D. dixoni*) in the Echinonëid stage, consisting of a large adoral primary, a small demi-plate, and a low adapical primary. In succeeding groups the last-named plate becomes a demi-plate, normally larger than the original demi-plate, and, with considerable irregularity, this condition is maintained as far as the ambitus. The irregularities consist, in the main, of "super-grouping" or the lapse of one demi-plate. Occasionally, tetrad-grouping appears, often in such a position that it compensates for a plate lacking in a contiguous group. The demi-plates are, in almost all cases, exceedingly minute, and near the ambitus, where their height is reduced very seriously, they are hardly adequate for the inclusion of their pore-pairs. Above the ambitus the congestion of plates is rapidly reduced, but complexity persists, albeit of a type differing from that normal to the adoral surface. Fairly regular alternation of primaries and *single* demi-plates occurs, the number of primaries gradually increasing in an apicad direction. Although the adapical region is largely composed of regular, fairly high, primaries, occasional spasmodic complexity may often appear (twice in the case figured), without any visible reason or connection with the main grouping-systems. These precocious reduced plates have a peculiar interest when compared with the structures of such phyletically distinct forms as Galeropygus and many other Nucleolitidæ, where occasional (usually single) demi-plates may occur at a considerable distance adapically from the hypophyllode or phyllode. The three specimens illustrated in figs. 4, 5, and 6 were selected from individuals found at different horizons, but with the same ambulacral length. They are here reproduced to show the small, but important, zonal modifications that occur in the species. Fig. 4, from an Upper Greensand (cylindrical) specimen, shows the greatest degree of ambital congestion, and has complexity extending for some distance above the ambitus. Even in the latter region the grouping is approximately

on the triad-plan. There are no precocious demi-plates. In fig. 5, from a Chalk-Marl (depressed) specimen, a considerable series of grouped primaries, followed by several "Pyrinid" groups, occurs between the peristome and the normal region. The congestion near the ambitus is less marked than in the previous case, but complexity is carried further up the area, and one series of precocious plates exists. The apicad primaries are proportionately higher than in the Greensand type. The original of fig. 6, a depressed example from the *H. subglobosus* zone, shows an unusual regularity of structure on the adoral surface, and an almost complete suppression of grouped primaries and "Pyrinid" groups near the peristome. In this specimen there are no precocious plates, nor do supra-ambital single demi-plates occur, but this feature is almost certainly due to the youth of the specimen. Since it was of the same size as the Greensand form, while the average size of specimens from the *H. subglobosus* zone is almost twice as great, it can hardly be doubted that this example has not attained full development. Fig. 1 is drawn to the same magnification, and shows the characters normal to adults from this horizon. In spite of this probable difference, one striking contrast can be seen between the Greensand and "Grey Chalk" forms. In the former a fair number of primary plates persist near the peristome, in the latter very few. This character is not perfectly regular in occurrence (as fig. 1 shows), but the average condition of the ambulacra of the two types is none the less indicated in figs. 4 and 6. It is noteworthy that in the latter form triad-grouping hardly extends above the ambitus, both in the young (fig. 6) and in the adult (fig. 1); but in the latter it is partly represented by "dyad-grouping," a condition rarely found in the *varians*-zone forms, and never, so far as my experience goes, in those from the Upper Greensand.

(*c*) The pore-fields.—The pores are minute and similar throughout. On the adapical surface they are uniserial, and placed very near to the adradial sutures. At and just below the ambitus they become extremely congested, and take on a quite intense triserial arrangement, which may be locally either biserial or quadriserial according to irregularities in the plating. Below the zone of congestion the pore-fields become almost straight again, and a uniserial sequence (with faint traces of triserial arrangement here and there) persists to the peristome margin. The pore-fields converge more rapidly than the adradial sutures (see Plate 66, fig. 3), and each adradial tract supports a row of prominent granules, one to each plate. The exiguous proportions of the demi-plates, which are hardly adequate for the inclusion of the pore-pairs, become thus emphasized by the occupation of much of their surface by ornament.

(*d*) Abnormalities.—The frequent irregularities that are indicated in figs. 1, 4 and 5 on the adoral surface seem to call for no special comment. It would be remarkable if so intensely complex a plating-system were carried out with perfect precision, especially since the relatively simple ornamentation is subject to much disturbance. However, in view of the almost mathematical accuracy with which triad combination

occurs in the Triplechinidæ, it is perhaps legitimate to suggest that the irregularity so prevalent in *D. cylindrica* may be an expression of morphogenetic plasticity. The occurrence of dyad grouping above the ambitus in adult forms of late geologic age I regard as a regular gerontic feature of great significance; its presumed meaning will be discussed in Section 3 (*e*), below.

There is, however, one type of irregular development which, whether normal or not, seems suitable for description here. A well-marked case is illustrated on Plate 66, fig. 7. This example is by no means unique, for out of 30 specimens from the same zone (*S. varians*) that I have examined, 13 show a character identical in style and localisation though much less clearly defined. The specimen (in the collection of G. E. Dibley, Esq.) is a small, depressed form, telescoped by pressure adorally, accidentally truncated adapically, and much encrusted with organisms. The ambulacra are very well preserved above the ambitus, excepting area II, which is largely obscured by a Plicatula. In accord with the character normal for the zone, plate-complexity extends considerably above the ambitus, but for an unequal distance in the different areas. In ambulacra I and V regular triad-grouping is followed by a fair series of "Pyrinid" or kindred plates. In area IV (and, by analogy with other specimens, in II also), there are fewer of the "Pyrinid" groups, while in area III there are none. The zone of complexity reaches nearly half-way up the adapical surface in I and V, and hardly a quarter of the distance in III. Area IV (and probably II) agrees fairly with I and V in this respect, but the extent of the complexity falls a little short. The anterior ambulacrum of *D. cylindrica* is in no way different in length, ornament or pore-characters from the other areas, and yet it very frequently differs from them in plating. This difference (rarely so marked as in the specimen figured) seems always to lie in a greater simplicity, as expressed by the number of ungrouped primaries on the adapical surface. I have never seen a specimen in which any of the other areas showed this quality. Slight as the irregularity is, it seems worthy of record partly on account of its frequency. and chiefly because it affects the anterior ambulacrum. In the Spatangidæ this area is almost always different from the rest, usually in a striking manner. In "Heart-Urchins," however, the heteronomy of area III is clearly associated with bilateral symmetry, and it is curious to find a similar tendency in *D. cylindrica*, where the radial symmetry produces an almost hemispherical test. There is no reason to believe that the feature was extended or even maintained in any near relatives or descendants of the species, so that it would appear to be a case of obscure parallel variation appearing at a time when such phyletically distinct groups as the Toxaster and Holaster series were developing a similar quality as an essential part of their structure.

### Family IV: Lanieridæ.

The two genera Lanieria and Dischlectypus, represented each by a single species, constitute a most peculiar group. Recently (Hawkins, 1913 *b*) I redescribed the

former genus from some of the original material, so that it is unnecessary to give more than a brief indication of the ambulacral structure. In practically all morphological features both genera seem to be typical Holectypidæ, and could almost be placed in the genus Coenholectypus, but in their ambulacral structure they are closely similar to the Echinonëidæ. I am convinced that their real affinities are with the former family, and that the appearance of Echinonëid ambulacral plating is a result of parallel evolution. Their ambulacral structure could be easily attained by amplification and elaboration of the Holectypoid plating; but the introduction of a posterior genital plate, with a functional fifth gonad (wanting in the Echinonëidæ) would involve the adoption of improbable methods of evolution on the other alternative.

## Family V: Echinonëidæ.

The Echinonëidæ possess the most complete complication of ambulacral structure found among the Irregular Echinoids, although the degree of reduction of the plates is not so intense as that locally developed in *D. cylindrica*, *Echinocardium cordatum*, or those forms that have true phyllodes. In the extent of the grouping, in the regularity of triad-structure in all genera, and in the remarkable absence of individual variation or abnormality, the family may be compared with the Triplechinidæ, which appeared at about the same period. Among many hundreds of specimens of Conulus that I have examined, not one showed disturbances of ambulacral plating (except of a trivial nature) unaccompanied by the effects of accident or disease. This perfection of development becomes the more striking when it is realised that no single ambulacrum of *D. cylindrica* has been seen in which unbroken triad-sequence occurred. Even in Amblypygus, where the proportions of the plates vary from long laths in the petaloid regions to almost "Bothriocidaroid" plates adorally, the normal plan of two unequal primaries enclosing a demi-plate is quite constant in all specimens and drawings that I have seen.

The systematic grouping of the Cretaceous Echinonëidæ is in a state of great confusion. Lambert (1911) has discussed and dismembered the genus Pyrina, but it is difficult to follow his meaning in regard to the separation of the various genera involved. Generic distinctions appear to be based largely on the "obliquity of the peristome," but since all the forms in the family with which I am acquainted have oblique peristomes (not excepting the species of Conulus), there seems a lack of precision in the various diagnoses. Conulus can be distinguished from the forms usually called Pyrina by its ambulacral characters, as will be shown below, but I am sceptical as to the merits of such genera as Globator and Pseudopyrina. However, for the present purpose it will be sufficient to use the term "Pyrina" (*sens. lat.*) for all the Cretaceous forms that cannot be referred to Conulus, since these species, with Echinonëus of later periods, seem practically identical as regards the structure of their ambulacra.

### Sub-family i: Echinonëinæ, (Plate 67, figs. 4–10).

Save for a few ontogenetically young plates near the peristome, and a slightly greater number of morphogenetically young plates near the apical system, the whole ambulacrum is built of plates arranged in triad-groups similar (except in combination) to the triads of Echinus. An orad primary of considerable height is followed by a much-reduced demi-plate, succeeded by an apicad primary, which, in the adult, is extremely slender. I have never seen a case in which this apicad primary became reduced. In a young Echinonëus, the transverse suture that separates the two primaries of a triad-group is usually directed in an orad and adradiad direction, so that the apicad primary is cuneiform, tapering perradially. This condition is normal (at least on the adapical surface) in the adult stage of Conulus; but in Echinonëus, and still more in "Pyrina," this transverse suture tends to become truly horizontal in direction. The perradial suture assumes a stiffly zigzag course, that may be described as "battlemented."

The pores are minute and similar throughout, except in Micropetalon (see below), and are practically uniserial. The pore-fields tend to converge towards the perradial suture near the peristome, as in *Discoidea cylindrica*, but it is rarely that any triserial arrangement can be detected. In connection with the pore-pairs of this sub-family, an interesting point arises. The orad biporous plates that characterise the ambulacra of all Atelostomatous Irregular Echinoidea are certainly not present in the Pygasteridæ and Holectypidæ, and have not been recognised in Discoidea or Conulus. Lovén (1875, Plate 14, fig. 128) shows a curious feature on one proximal plate in *Conulus rhotomagensis*, the two pores of the pair being widely separated. Were it not that the podial pores of Conulus are always paired, the condition that he illustrates might well be taken as representing a "biporous ambulacral" bearing, like that of a Spatangid, two single pores. It is usual to regard Echinonëus as a form with biporous ambulacrals, but the careful drawings made by Westergren (1911) show that, if such structures are present, they possess quite anomalous features. In Plate 67, figs. 8, 9, and 10, copies of Westergren's drawings are given, showing ontogenetic stages in the growth of the proximal parts of the ambulacra. In the very young stage (fig. 8) the vestigial perignathic process obscures the pores, but there is no sign of any "biporous" plate. In a later phase (fig. 9), when the processes have disappeared, there are normal pore-pairs in each proximal plate. But the small peristomial grooves (? vestigial branchial incisions), which notched each column in the earlier stage, are now reduced to one, which makes a small inlet into the margin of the plate which, according to Lovén's law, should be biporous in a Spatangid or Cassiduloid. In the adult (fig. 10) this notch has disappeared as such, and three pores, two evidently paired, perforate the plate in question. Westergren shows no case of a "biporous" plate in Echinonëus, in which there are two pore-*pairs*, and, from a study of the scanty material at my disposal, I agree with him that the "biporous ambulacral" includes one pore-pair and an odd single

pore. May not this latter be the enclosed relic of the surviving "branchial incision"? In the Collyritidæ, and other forms that have persistent pore-pairs, the biporous plate contains two complete pairs, each in a peripodium, so that there is a definite difference between a normal biporous ambulacral and the analogous structure in Echinonëus. On the evidence available, I am inclined to answer the question asked in a previous sentence in the affirmative, and to suggest that Echinonëus has no true biporous ambulacrals.

The case is otherwise in the small, unique form described by AGASSIZ and CLARK (and redescribed by WESTERGREN) as *Micropetalon purpureum*. In that form (here Plate 67, fig. 4) there is a perfectly definite biporous plate in each area, normally provided with two pore-pairs. There are, however, serious doubts as to the systematic validity of Micropetalon. It may be, as WESTERGREN suggests, a post-larval stage in the development of some other type. The character of its ambulacral plates resembles that of the young *Echinonëus* (fig. 5) far more than that of the adult (fig. 6), and conforms fairly closely to that of Conulus. The faintly sub-petaloid character of the apical pores, and the relatively large size of the tubercles, also point to the youthfulness of the specimen. I should be inclined to regard Micropetalon as an early stage in the development of some non-Holectypoid descendant of the Amblypyginæ, but more evidence is required before such a suggestion can be given in any but a speculative sense.

Sub-family ii: CONULINÆ. (Plate 67, figs. 3, 11, and 12.)

As regards plating-structure, the ambulacra of Conulus agree with those of the Echinonëinæ very closely, particularly with those of the young Echinonëus (fig. 5). The relative height of the plates, and the usual obliquity of the course of the internal transverse sutures of the triad-groups serves to distinguish the structure from that of "Pyrina," both features apparently resulting from less advanced (or more regressive) evolution. It is usually very difficult to distinguish the sutures on the adoral surface, owing to the great congestion of ornament; primary and secondary tubercles, granules and "glassy tubercles" occurring in great profusion. I have never found a specimen in which weathering has displayed the sutures on this surface, although such aids to investigation are frequent on the adapical surface; but there seems no reason to believe that true combination occurs. The original specimen from which fig. 3 was drawn was partly decorticated, so that in places the sutures are drawn from impressions on the internal mould. The original of fig. 12 is the only one in which, by artificial etching and staining, I have been able to display the sutures with any clearness, but there is no reason to doubt that it is perfectly typical. In fig. 11 a retarded primary (cuneiform) replaces the usual demi-plate in one case. Such a development recalls the "Diademoid" triads sometimes found in Echinus, but it is of very rare occurrence.

Near the peristome the pore-pairs, which are elsewhere perfectly uniserial, become

very strongly triserial in arrangement, the character being emphasised by the existence of well-marked depressions in which the oblique series are situated. As far as the pore-pairs are concerned, this arrangement is suggestive of incipient phyllode-structure, but there is no accompanying change in the nature of the plating. Nevertheless, this triserial plan of the proximal pore-pairs seems to constitute a sound distinction between Conulus and "Pyrina." It is most definitely marked in *C. albogalerus* among British species, and seems to progress in intensity as the genus is traced upwards through the zones of the chalk. But even the low-zonal forms of *C. subrotundus* and *C.* (*?*) *rhotomagensis* have quite clearly triserial pores.

### Sub-family iii: Amblypyginæ.

The genus Amblypygus, which bears a close superficial resemblance to the Echinolampidæ, has typical "Pyrinid" ambulacral plating. But in the character of its podial pores it marks a great and systematically embarrassing advance from the Holectypoid condition. Over the greater part of the adapical surface the pores are completely heterogeneous, with the result that a fully petaloid character is produced. There is no complementary phyllodal development adorally, and the oblique peristome compares with that of Echinonëus. It is, however, solely on the nature of its ambulacral plating (as beautifully portrayed by Duncan and Sladen, 1884), that I venture to include the genus among the *Holectypoida*. The apparently nearly related Oligopygus, according to Clark and Twitchell (1915), has primary plates only, but these are irregular in shape, and often imperfect in alternation. The possible phyletic position of the sub-family is further discussed in Section 3 (*c*) below.

## (2) The Ascertained and Probable Functions of the Holectypoid Ambulacrum.

It is clear that any conclusions as to the uses of the tube-feet of the *Holectypoida* must be almost entirely hypothetical. In one case only, that of Echinonëus, is there a possibility of actual observation of habits and habitat; and the value of this exiguous evidence is seriously reduced by the dissimilarity in general structure between *E. cyclostomus* and the Jurassic *Holectypoida*, and might be altogether denied by those who do not follow the present writer in the inclusion of the genus within that Order. There are, however, two lines of argument, based upon independent series of observations, from which the possible ambulacral functions can be deduced with some measure of confidence. On the one hand, the known association of certain functions with definite types of structure in recent forms may be employed, by inverse argument, as a basis for the indication of the purposes of the ascertained structures of the Holectypoid ambulacrum; and on the other, a recognition of the lithological qualities of the deposits in which the fossils are found will afford a clue to the opportunities for the exercise of various podial

functions available for Echinoids living under the environmental conditions thus determined. The substantial agreement between the conclusions to be drawn from these independent arguments must assuredly indicate that they represent a reasonable approximation to the true solution of the problem. The results obtained have important bearings on the morphogenetic arguments which conclude the paper, so that the subjoined paragraphs are introductory to that section, and at the same time are a direct sequel to those of Section 2 (*e*) of Part I.

*Echinonëus cyclostomus*, according to H. L. CLARK (as quoted by WESTERGREN, 1911, p. 42), lives among stones and weed at about low-water mark. In Jamaica it inhabits a "sand-flat within the reef," buried in the sand under fragments of broken coral-rock. "In rare instances, specimens were found clinging to the rock" by the adapical tube-feet. "The tube-feet of Echinonëus are used to hold sand-grains and particles of dirt close against the test." "Both spines and tube-feet appear to be used in locomotion." It is clear from this account that Echinonëus has no great powers of adhesion by its podia, but rather seeks sheltered lagoon water; even there its habits are markedly retiring.

The Pygasteridæ show a progressive simplification both of pores and plating-structure. The close series of slightly dissimilar pore-pairs on the adapical surface in Lower Jurassic forms seem to represent rudimentary petals; while the more widely spaced, similar pore-pairs of the adoral surface, set in plates that show some degree of complexity (albeit none of combination) seem more adapted for the usual adhesive function. The distribution of the pores on the test, with the greater number on the adapical surface, might be taken as an indication that the respiratory function was the more important, especially as the adoral plate-complexity does not attain that true combination which alone can strengthen the areas in their resistance to strain, while the pore-pairs are hardly displaced from an uniserial arrangement. In Pileus, on the other hand, the markedly biserial character of the apicad pore-pairs might suggest an adaptation to mechanical effort; but this suggestion would be qualified by the nature of the pores, which, though similar, are large and elliptical, two features that are quite unlike those found in the pores that transmit adhesive podia in the Regular Echinoidea. Perhaps the apicad podia of Pileus were equally respiratory with those of Pygaster, the leaf-like podia being of a somewhat different shape. The podial pores are strikingly like those of the petals of the Spatangidæ, but much more densely crowded. The biserial grouping may be a device for the accommodation of great numbers of podia which, if in a continuous series, would be too closely packed for efficient aëration. On the adoral surface the small, strongly triserial pore-pairs certainly suggest the exercise of adhesion by their podia—a function which life among coral-reefs would demand in so large a form as Pileus if any exposure to wave-action was incurred. In the Cretaceous members of the family the pore-pairs are minute and practically similar and uniserial throughout, while there is little, if any, complexity in the ambulacral plating.

There is thus no indication of any special adaptation for respiratory purposes (podia cannot avoid performing that function to some degree), and the small size of the pores would suggest that the slender podia that passed through them could not have possessed any great power of adhesion. Perhaps the crowded ornament of Macropygus and Anorthopygus (indicative of abundant and fairly massive radioles) may be associated with ambulacral failure in this respect.

As far as can be ascertained from the facts of geological distribution, the Pygasteridæ appear to have been exclusively inhabitants of shallow water, and probably to have been restricted to the littoral zone. Their remains are found in the limestones and sandstones only in the Lower Oolites, and although *Pygaster macrocyphus* occurs in the Kimmeridgian, it is not found in the Kimmeridge Clay. On the whole, the clays of the Oolitic period represent the deposits of more open water than the sands or oolitic and coralline limestones, many of which are of almost inter-tidal origin. The distribution of the Cretaceous members of the family gives similar evidence. Both Macropygus and Anorthopygus are to be collected only in the "Greensand" facies of the Cretaceous deposits. The latter genus is, so far as present experience goes, restricted in Britain to the Haldon Hill drift and the Hibernian Greensand, never having been found in the chalk proper. It is thus reasonable to claim for the Pygasteridæ as a whole a general habitat not very different from that of Echinoneus and most of the Clypeastroida. The absence of true petaloid developments in the extinct family may be considered as an indication of imperfect adaptation to surroundings different from those of its Regular ancestors. Although the earlier Pygasteridæ show a tendency to develop suitable ambulacral modification, the attempt was not maintained, and the family died out in Cretaceous times with podia that had largely lost their earlier adhesive function and failed to acquire a new one.

Most of the suggestions made for the Pygasteridæ hold good for the Holectypidæ. There is less indication of any petaloid qualities in the apicad podia, though this is in some degree compensated by the great numbers of apparently tubular podia that were retained on the adapical surface. On the other hand, a considerable reduction in the numbers on the adoral surface was thereby brought about, and the few podia that occurred in that position in such an extreme case as that of *Holectypus "depressus"* in the Cornbrash, although situated in grouped plates, would be insufficient to enable their owners to resist any violent disturbing influences. The marked crowding of the pore-pairs that occurs near the ambitus in most forms of the family is probably directly associated with the exercise of special functions by the podia of that region. In forms with flat adoral surfaces that lived on relatively smooth sand, the podia near the peristome would have little freedom for action of any kind, while the sharp ambital angle would remove the apicad podia from any normal contact with materials to which they could adhere. Only at the ambitus would freedom and adhesion be practicable. Moreover, podia so situated

could use the sensory qualities that are always potentially present in them with the same success and advantage that attach to antennæ in other animals. The latter function is, perhaps, the more probable for the ambital podia, since the ambulacral plates of that region are, by their congestion, less suited than usual to withstand mechanical strain. In view of the inadequacy, either of numbers or arrangement, of the podia for the adhesive efforts required for locomotion, that function would devolve upon the radioles of the adoral surface, and it is suggestive to find that the tubercles below the ambitus are disproportionately larger than those adapically placed. The Holectypidæ would seem, therefore, to have adopted the Clypeastroid or Spatangid mode of progression, and to have left their podia to perform the two inevitable functions of respiration and sensation, without any specialization for those purposes of a kind that affected the character of the pore-pairs. The geological distribution and probable habitat of the Holectypidæ are both very similar to those of the Pygasteridæ.

In a discussion of the podial functions of the Discoidiidæ, it will be sufficient to consider the extreme case of *D. cylindrica*. The smaller species differ in ambulacral characters only in degree, and the differences will not, therefore, affect arguments of this kind, although they may prove to be of great importance in morphogenetic considerations. An outstanding feature of the ambulacra of *D. cylindrica* is the extraordinary numbers, and extreme congestion, of the plates and pores. In proportion to its size, the corona of this species shows vastly greater plate-complexity, and considerably greater pore-crowding, than that of any other Echinoids, excepting, perhaps, some of the later Palæozoic types. Both qualities are at their maxima on or about the ambitus, so that there is a similarity in that respect to the Holectypidæ. The plentiful development of demi-plates, and the departure from uniserial sequence of the pores, might perhaps be taken to imply adaptation for an adhesive function, but I believe that such a view would be mistaken. In the first place, there is no combination of the complex plates, so that the poriferous tracts, already weakened by the very numerous and close-set perforations, are rendered still more fragile by the concentration of sutural tissue that results from the congested structure. Secondly, the pores are exceedingly minute, so that the podia must have been mere filaments; and, although this character might be counteracted in some degree by their great numbers, such slender proportions do not occur in those podia of recent forms that exhibit any adhesive efficiency. Lastly, *D. cylindrica* must have lived in surroundings which, in the latter part of the history of the species at least, would make podial locomotion practically impossible. Marly ooze, such as that which surrounded the species in Lower Chalk times, would render abortive the most vigorous efforts at progression by such means. The concentration of large tubercles around the ambitus seems to point to the radioles as the chief locomotive organs. The biserial (or, rather, irregularly multiserial) arrangement of the pores near the ambitus seems comparable with the analogous displacement of the

apicad pores of Pileus, designed in this case to prevent the crowded, filamentous podia from becoming entangled in one another; and even to ensure that the pore-pairs, small though they are, shall be separated by bars of stereom. But, if a locomotor function is denied to the tube-feet of *D. cylindrica*, there is an undoubted difficulty in finding a cause for the extraordinary numbers of podia developed, especially on the adoral surface. That surface is so flat, save for the small but deep peristomial invagination, that it must have been very nearly in contact with the ooze of the sea-floor, so that its podia could hardly be of service for respiration. In the absence of any closely comparable structures in living forms, an attempted explanation must needs be conjectural, and it is in that sense that the following sentences must be read. An organism living on an ooze-surface must inevitably be normally microphagous in habits, even if it be endowed with jaws that could be used if occasion offered. It would therefore be an advantage to the animal to have abundant means of selecting nutritious particles from among the mass of inedible material over which it passed, so that the very numerous, slender adoral podia of *D. cylindrica* may have performed the function usually ascribed to those of phyllodes or to the ragged tube-feet that surround the peristome of a Spatangid. Added to this sensory activity there might well be a feebly prehensile function in the podia, so that they could pick up and pass to the mouth those particles that had been selected. The rapid convergence of the pore-pairs towards the peristome, and the palisade of large granules (presumably supporting a row of small radioles) along each adradial tract, might be adaptations to such a "Pelmatozoic" habit of feeding. The suggestion is made with the less diffidence on account of the remarkable character of the anterior ambulacrum of *Echinocardium cordatum*. In that advanced Spatangid (Plate 69, figs. 4 and 5) the plating of the petaloid region of area III is even more elaborate than that of Discoidea, and the podia that project from it are used, according to MacBride, to catch small prey, and pass it down the anterior sulcus to the mouth. Whatever may have been the true functional uses of the podia of *D. cylindrica*, I believe that the elaborate plating-structure is the expression of a morphogenetic trend of great importance (see Section 3 (*c*)).

There is every reason to believe that the ambulacra of the Echinonëinæ were employed similarly to those of Echinonëus. The identity of structure gives *primâ facie* support to such a view, and the restriction of the forms here grouped under the name "Pyrina" to littoral facies of the Cretaceous deposits affords confirmation. The habitat of Conulus was undoubtedly different from that of Echinonëus. The earlier species, such as *C. rhotomagensis*, may have inhabited shallow water not far from the coast, but the later forms, typified in this country by *C. subrotundus* and *C. albogalerus*, are abundant only in those zones of the chalk which seem to have accumulated in relatively deep and open water. The extreme rarity of specimens of Conulus in the zone of *Holaster planus* seems to indicate that the genus had definitely abandoned shallow water by that time. The

markedly triserial arrangement of the adoral pore-pairs, though unaccompanied by any special plating-structure, invites comparison with the phyllodes of other groups. There is not the same structural need for displacement of the pore-pairs as exists in the ambital parts of Discoidiid ambulacra, so that the adoption of a triserial grouping would seem to be associated with some local functional peculiarity. That such an activity was connected with feeding habits would appear likely from its restriction to the podia bordering the peristome; and this assumption would apply equally to phyllodes. Possibly the proximal orad tube-feet of Conulus were used partly for retaining the food which the enfeebled jaws could masticate but slowly, and partly for "tasting" the material collected. Such uses would be closely akin to those believed to be made of the phyllodal podia in the Cassiduloids; and it is perhaps more strange to meet with no such provision in the other Echinonëidæ than to find it in this group. The rudiments of phyllodal plating-structure are present almost throughout the ambulacra of Conulus, and, if the genus had any phyletic descendants, true phyllodes could readily have been developed from the already triserial parts of the areas.

To summarise the foregoing arguments:—The Pygasteridæ alone of the Jurassic *Holectypoida*, seem to have begun to develop branchial podia in rudimentary petals, but even this family abandoned the attempt in the Cretaceous period. The Holectypidæ and Discoidiidæ have ambital congestion of pores, probably associated with the sharpness of the distinction between the two surfaces of the test, which reduced the opportunities for normal functional activity of the podia except at the margin. *Discoidea cylindrica* shows an extraordinary multiplication of podia, without any evidence of their local specialisation, and may have used those of the adoral surface for the transference of food particles to the mouth after the manner of *Echinocardium cordatum*. The Echinonëidæ, with evenly distributed podia, employ the tube-feet in such feeble expressions of adhesion as the retention of small rock-particles as a protective covering for the test (with subordinate locomotor function), while Conulus shows some slight tendency towards phyllodal specialisation. Probably the exercise of a respiratory function was the chief use of the Holectypoid podia, although the absence of special petaloid development shows that it was only adopted incidentally. The Jurassic types had greater powers of adhesion than the Cretaceous forms, while the only living type has adopted the burrowing habits associated (in the Spatangidæ) with an almost complete loss of adhesive power in the podia.

### (3) The Evolution of the Holectypoid Ambulacrum.

In this, the concluding section of the paper, the facts, principles and hypotheses that have been described and enunciated in the foregoing pages are combined in an endeavour to determine the morphogenetic relations existing between the ambulacra of the *Holectypoida* and those of other orders. In arguments of this nature it is inevitable that a high proportion of the personal element should be introduced, but pains

have been taken to restrain it. Principles of evolution that have an application over far wider fields than that of ambulacral morphogeny are involved. Further, it is practically impossible to exclude occasional phylogenetic arguments, although these are subordinated to morphogenetic considerations. The various trends of evolution indicated are not of necessity lines of phylogeny; in many cases, however, there is reason to believe that the two "genealogies" are parallel if not coincident.

### (a) *Within the Order.*

With one exception, all manifestations of ambulacral complexity in the *Holectypoida* show some degree of "triad-grouping." The exception (*Discoidea cylindrica*) is only partial, for the bulk of the complication is triadic, although liable to frequent irregularity. It is thus clear that a fundamental uniformity of ambulacral morphology underlies the evolution of the whole group.

There are four chief modifications of ambulacral plating in the Order:—These may be named from their earliest known possessors as the Plesiechinid, Pygasterid, Pyrinid and Discoidiid (exclusive of small species). The probable relations between the four types can be considered first. The Plesiechinid type (Plate 65, figs. 1 and 7; Plate 67, fig. 1), which consists of orad triad-grouping with but little plate-reduction, and simple primaries (apart from tubercle interference in early forms) throughout the ambital and adapical regions, occurs in the Pygasterinæ, (?)Pileinæ, Holectypidæ, and *Discoidea subucula*. Since Plesiechinus is in all respects the least "Irregular" genus of the order, and also the earliest, it seems certain that this quality may be taken as morphogenetically primitive. The Holectypidæ show no other type of structure, but some forms of the Pygasteridæ, and most of the Discoidiidæ, present differences which result, presumably, from the modification of the Plesiechinid type.

The Pygasterid type (Plate 65, fig. 3), in which plate-grouping, except for that under the influence of the tubercles, is almost absent, occurs only in the later Pygasteridæ. The ornament is still "triadic," but the plating has become simplified. Such a change was undoubtedly reversionary, whatever may be the views held as to the immediate ancestry of the *Holectypoida*, since there can be no doubt that some Cidaroid form was on their line of descent; and, although the ornament retains "Diademoid" characters, the plating of the orad parts of the ambulacrum of *P. semisulcatus* is essentially Cidaroid in quality. The structure is closely comparable with that of *Orthopsis*, and the remarks of Bather (1909, pp. 108–109) on that genus are interesting in this connection. Such simplification could hardly be expected to precede further elaboration, so that the Pygasterid type of ambulacrum must be considered to indicate a side-line of evolution divergent from the main trend of morphogenesis in the *Holectypoida*.

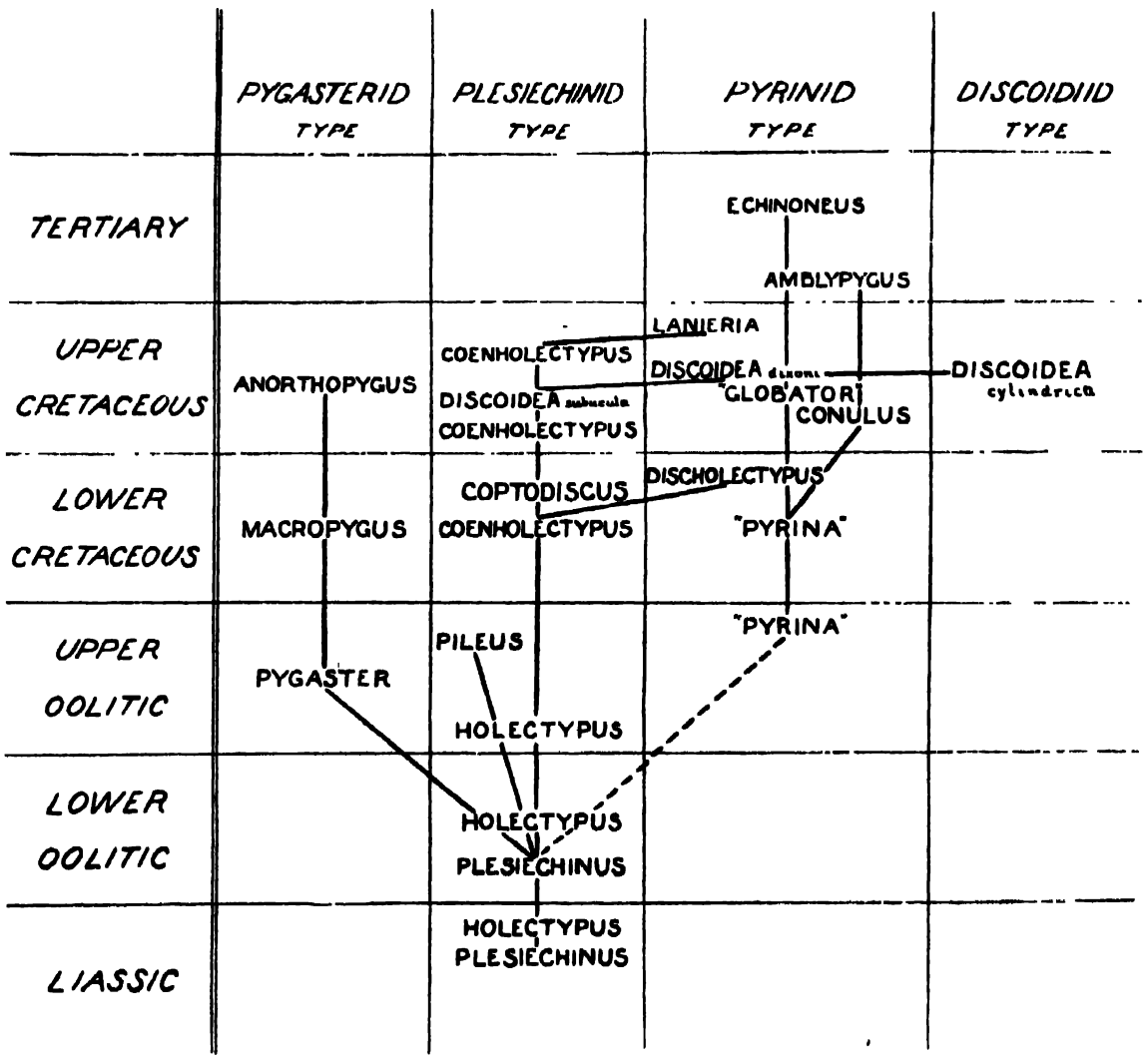
The Pyrinid type (Plate 67, figs. 2–12), which consists of very regular triad grouping on an approximately "Echinoid" plan, with the persistent development of a demi-plate in each group, is seen in its simplest expression in *Discoidea dixoni*, and is

universal and regional in the ambulacra of the Lanieriidæ and Echinonëidæ. The occasional production of demi-plates in the triad-groups of Plesiechinus, and their more frequent occurrence in the Holectypidæ, would seem to indicate that the morphogenetic descent of the Pyrinid ambulacrum passes from the latter family through the stage represented in *D. dixoni*. This does not, however, imply that the Echinonëidæ are phyletically descended from the smaller Discoidiidæ; a direct sequence from the Holectypidæ, or perhaps from the *Plesiechinus*-stock, is more probable, with the Discoidiidæ in a parallel line of evolution. It is interesting to note that the Pyrinid type of grouping is the most static of ambulacral structures in the order. Not only do most of the later members possess it, but cases of irregularity in its development are very rare. This is surprisingly in agreement with the condition found among the Regular Echinoidea, where the "Echinoid" type of combination characterises a very large series of Cretaceous and Recent forms, and seems less liable to abnormality than any other type. The two sets of structures are, moreover, practically synchronous in their appearance, both occurring for the first time (in a definite form) in the Lower Cretaceous. This suggests that morphological evolution of the ambulacra may have proceeded at the same rate (with difference in the quality of plate-combination) in the two homogenetic but otherwise very divergent orders of Diadematoida and *Holectypoida*. The appearance of true "Pyrinid" structure in the Lanieriidæ, which seem to be a small group of forms phyletically descended from the Holectypidæ, and quite independent of the Echinonëidæ, may indicate a third parallel line; but, on the other hand, the family may be related to the smaller Discoidiidæ.

The Discoidiid type (Plate 66) is remarkable for its extreme complexity and dual nature. The plate-grouping on the adoral surface and ambitus is essentially "triadic," and to judge from the morphogenetic sequence shown in the orad parts, would seem to be the result of intense acceleration from an incompletely Pyrinid structure such as that of *D. dixoni*. It is thus traceable back to the Plesiechinid type. But in the gerontic forms, particularly from the upper part of the Lower Chalk, the occurrence of alternate primaries and demi-plates is too constant and regular to be regarded as the product of abnormality. In a very large cylindrical specimen from the zone of *H. subglobosus* (text-fig. 3, p. 463), in the collection of G. E. Dibley, Esq., which was not available when Plate 66 was drawn, column *a* shows no less than 14 demi-plates alternating (with one exception) with single primaries. They are followed adapically by a curious recrudescence of simple triad grouping in this case, but that is unusual. This development is something new in the order, and is clearly quite independent of the ancestral triad-character of the other cases of complexity. It involves only those plates which, in all but fully developed Pyrinid types, are still primaries, and thus is restricted as a regular structure to the adapical surface. It has no known morphological ancestry or descent within the limits of the order. The frequent, and often extreme, irregularity of the

normally "triadic" portions of the areas is also worthy of comment. Although lapses from perfection might be naturally expected in so elaborate and congested a structure, the fact remains that no such irregularity occurs in those Echinoids whose complexity approximates to that of *D. cylindrica*. It seems explicable only as an expression of the morphogenetic instability which might be associated with transition from one stage of complexity to another, but that other is plainly not an Holectypoid type.

The foregoing considerations may be summarised in the following diagram, which, it may be well to repeat, is not intended to represent true phyletic connections, although these are probably indicated approximately :—




TEXT-FIG. 2.—Table showing the inter-relations of the four types of ambulacral structure in the *Holectypoida*. The middle line in each column represents a more or less static evolution; divergences from it indicate progression or reversion. The line ending in *Discoidea cylindrica* should not pass through *D. dixoni*, but arise independently in *D. subucula*.

### (b) *Pre-Holectypoid Evolution.*

In the light of the descriptions and arguments given in Part I of this paper, the search for the morphogenetic "ancestry" of the Holectypoid ambulacrum is soon successful. Such an inquiry becomes narrowed down to the problem of the origin of the Plesiechinid type of ambulacrum, since, if the conclusions in the foregoing section are correct, the ambulacral qualities of the Holectypoida can be traced back, directly or indirectly, to that type of structure. Since Plesiechinus itself is the earliest, or one of the earliest, of the order to appear, and is undoubtedly the most primitive in general characters, the nature of the search is still further simplified. The type of ambulacral structure that immediately preceded that of Plesiechinus would be expected to resemble it very closely, in view of the small departure from Regular qualities shown by the other morphological characters of the genus.

The ambulacrum from which that of the earliest Holectypoida could be derived should possess the following characteristics :—(*a*) Straight and lanceolate, (*b*) tuberculate in "triad" fashion, (*c*) largely built of simple primaries, but with some complexity towards the peristome, (*d*) the complexity in the stage of association marked by grouping without true combination, (*e*) the groups consisting of dyads with the orad member large and tuberculate, alternating with separate, single primaries. Further, such an ambulacrum must have been in existence during or shortly before the Liassic period.

There can hardly be any doubt that the preceding paragraph represents an almost complete diagnosis of an early, though not absolutely primitive, Diademoid ambulacrum. Indeed, the ambulacra of Plesiechinus are typically Diademoid, save for the relative proportions and numbers of the tubercles and the very faint tendency to a sub-petaloid structure adapically. As far as the plating-structure is concerned, the forms ancestral to the Holectypoida will have passed beyond the Diplocidarid and Saleniid styles of grouped dyads, and have reached the stage which is represented typically in parts of the areas of the Acrosaleniidæ, intermediate between dyad and triad grouping. The absence of any true triad-groups would imply a less advanced structure than that of the Oolitic species of *Acrosalenia* or *Hemipedina*, but the presence of additional plates between the dyad-groups would involve a progress beyond the stage shown in the Triassic "Diadematoid ambulacra" described by Bather (1909). Since the Liassic period intervenes between the Triassic and the Oolitic, the chronological sequence proves sufficiently convincing. The absence of combination, even at the peristome, and the great preponderance of ungrouped ambulacrals in the areas, are further features that demand a less specialised origin than those known in Oolitic Diademoida.

In view of the history of the development of ambulacral structures sketched in Part I, it may be confidently stated that the Plesiechinid ambulacrum must have been evolved from an area which was definitely Diademoid, but which was less

advanced in the *amount* of complexity than that of the Saleniidæ, and less advanced in the of *degree* complexity than that of Oolitic forms of Hemipedina or Acrosalenia. As far as ambulacral characters alone are considered, almost any Liassic Diademoid might be expected to possess the requisite quality, and it would be premature here to attempt to determine the actual genus, or even the family, most likely to have given rise to the *Holectypoida* by direct descent.

It is interesting to note, in view of the conservatism of the *Holectypoida*, that the incorporation of the single primaries with the dyad-groups is postponed until the Cretaceous period; while the resulting triad-groups, which resemble those of Echinus in many respects, retain this originally separate plate as a primary in all groups except those of the elaborate ambulacra of *Discoidea cylindrica*.

### (c) *Post-Holectypoid Evolution.*

(i) While the time of the origin of the *Holectypoida* occurred in stratigraphical stages whose Echinoid faunas are inadequately known, the period of their specialisation corresponds to those rock-systems that are most replete with palæontological evidence. There is thus an opportunity for more precise knowledge of the relation of the Holectypoid ambulacrum to contemporary and subsequent ambulacral types. It is important to realise, however, that the *Holectypoida* is not the only order of Irregular Echinoidea that appeared in the Liassic period. Omitting further reference to the problematical Loriolella (see FUCINI, 1904), at least one non-Holectypoid genus, Galeropygus, occurs in the Upper Lias. In view of this stratigraphical association, it is necessary first to discuss the possibilities of relationship between the ambulacral structures of Plesiechinus and those of the primitive Nucleolitoida. There can be little doubt that Galeropygus bears the same phyletic relationship to Nucleolites and Clypeus as that which Plesiechinus bears to the *Holectypoida*.

The ambulacrum of *Galeropygus agariciformis* (Plate 68, fig. 1) shows important resemblances, and no less important differences, when compared with that of Plesiechinus. The chief resemblances consist of the following characters:—(*a*) The ambulacra are straight and fairly regularly lanceolate; (*b*) the adapical parts are very feebly sub-petaloid; (*c*) the ambulacrals are simple primaries from the apex to a region quite near the peristome; (*d*) in the orad parts where complexity occurs the plates are grouped on the triad-plan. This series of similar qualities undoubtedly suggests that Galeropygus and Plesiechinus are homogenetic, even if they are not more intimately connected. The main points of difference are as follows:—(*a*) The areas of Galeropygus are proportionately very narrow throughout their extent; (*b*) The sub-petaloid adapical parts comprise plates of more slender proportions than those towards and below the ambitus; (*c*) These "mid-zonal" plates are almost "Bothriocidaroid" in shape; (*d*) The orad region of complexity is more concentrated, and more elaborate, constituting a well-marked hypophyllode; (*e*) The

tubercular ornament is fine-grained and diffuse, with but obscure traces of a "triadic" sequence. All of these differences might be regarded as accelerations from the Plesiechinid condition, even if, according to the general plan of ambulacral morphogeny, they present regressive qualities. There would be nothing surprising in a stock (such as that initiated by Plesiechinus) which was in the main conservative, giving rise to a side-branch of more active evolutionary character. Indeed, the rate of acceleration of the Discoidiidæ and Echinonëidæ in Cretaceous times was, as regards the ambulacra, far more rapid in many respects than that which could have produced Nucleolitid from Plesiechinid structures. As far as stratigraphical evidence is available, Plesiechinus and Galeropygus are practically synchronous in appearance. This fact, while not excluding the possibility of the derivation of the latter through the former, is perhaps more suggestive of their contemporaneous origin from a common stock. At least it shows that the differentiation of the Plesiechinid type cannot have progressed far before the Galeropygus-series arose. While recognising that the direct evidence as to the phyletic relationship between the two genera is fairly evenly balanced, I incline to the view that the Nucleolitid stock diverged from the Holectypoid after the latter had definitely separated from the Diademoida. This opinion is not based upon ambulacral characters alone, and so cannot be discussed in detail in this place, but it receives considerable support from some features shown in the ambulacra of Nucleolitidæ that are more advanced that Galeropygus. From a phylogenetic standpoint the two alternatives are so similar that they cannot have much significance, but morphogenetically considered they would introduce the operation of somewhat different principles.

In Plate 68, figs. 2 and 3, the ambulacra of two Oolitic species of the Nucleolitidæ are analysed. It is plain that there are two features in which these late descendants of Galeropygus show marked, but varying, advances beyond the stage of ambulacral specialisation reached by that early form. The petals become more pronounced and at the same time more restricted. The hypophyllodes also become more definite, both in their apicad limits, their plating-structure, and the dislocation of their pore-pairs. Whereas the petal of *Nucleolites scutatus*, from the Corallian, is more completely developed than that of *N. quadratus*, from the Cornbrash; the hypophyllode of the older type is far more elaborate than that of the Upper Oolitic species. Except for the absence of expansion and depression, the orad parts of the ambulacra of *N. quadratus* merit the name of phyllodes, while those of *N. scutatus* show very little reduction of the plates. This tendency towards a simplification of plate-complexity in *N. scutatus* is particularly suggestive when its results are compared with the truly extraordinary structures of Trematopygus (Plate 68, fig. 4). There can hardly be any uncertainty as to the close relationship between Trematopygus and Nucleolites. The two were originally classed under the same generic name, and even now some authors accept Trematopygus merely as a sub-genus of Nucleolites. The only species that I have been able to study in detail is *T. faringdonensis*. The

species occurs in one facies only of the well-known Aptian "Sponge-Gravels" of Coxwell, but the peculiar lithological nature of that deposit is admirably adapted for the display of Echinoid sutures. Secondary additions of calcite have been deposited on all available calcareous bases, and elsewhere (finally over all) a thin film of dark-red iron oxide has been spread. This process has raised the surfaces of the coronal plates well above their original levels, and has left the sutural lines unfilled. By gently scraping the surface and rapidly cleaning with hydrochloric acid, it is possible to make the plates appear white, while the sutures are left sharply defined as dark-red lines. I know of no conditions of fossilisation better calculated to make the tracing of sutures at once easy and certain. There is, therefore, no room for doubt that the ambulacral structure illustrated in fig. 4 is absolutely the true one, except in the part where the lines are dotted, and even there the indications of sutures are reasonably plain. I have studied six specimens, and the structure of all of them was practically identical. Morphologically, it is interesting to note that the amount of plate-complexity is greatest in area III, which is the shortest, and least in the longest areas I and V. But the character of the complexity is most unexpected. The relations of the plates are surprisingly like those that characterise Conulus; and, to make the comparison with Holectypoid structure more complete, two triad-groups in area IV are precisely similar to those that occupy the greater part of the adoral surface of *Discoidea cylindrica*. When the correspondence in geological age between Trematopygus and the early Echinonëidæ and Discoidiidæ is taken into account, a further coincidence appears. To suggest that there is any close phyletic link between Conulus and Trematopygus would be absurd, but some explanation of their remarkable ambulacral similarity must be forthcoming. In the first place, it is suggested that the extended range of plate-complexity is a result of continuation of the simplification of the hypophyllode indicated in *Nucleolites scutatus*. The degree of concentration of the hypophyllode has become lessened, and its nature more diffuse. But at the same time a great increase in the number of plates affected by complexity has occurred, so that, in this respect, Trematopygus would be related to Nucleolites much as the Echinonëid type of ambulacrum is to the Plesiechinid. (As an additional correspondence, the oblique shape of the peristome in Trematopygus may be cited.) The principle of parallel and synchronous morphogenesis in homogenetic groups is abundantly illustrated by Palæontology, but it is usually restricted to phyletic series of considerable intimacy. If the Nucleolitid series be presumed to have branched off from the Holectypoid stock, the ambulacral structure of Trematopygus seems explicable on that principle, though remaining none the less surprising. But if Galeropygus, which must surely be claimed as the parent of the Nucleolitidæ, were evolved from some Diademoid ancestor independently of Plesiechinus, the appearance of typically Holectypoid structures in its descendants would hardly be credible. Much more study of the ambulacra of the Nucleolitoida is needed before the suggestions made above can be considered proved, but they seem

to be the only ones possible, in the light of facts and morphogenetic tendencies as yet known.

A somewhat similar, though far less extraordinary, feature is illustrated in Plate 68, fig. 5. *Clypeus sinuatus* has petals in the most complete stage of development attained in the Jurassic period (see Plate 68, fig. 6), and also possesses well-developed phyllodes. But, in the parts of the ambulacra that intervene between the two specialised extremities, the characters shown are distinctly Holectypoid. The pore-pairs are triserial, and the tuberculation is very regularly repeated on every third plate. The plates concerned are tending to revert to Bothriocidaroid proportions, showing a considerable difference from those similarly situated in Galeropygus, and with this reversionary character there appears a regularity of ornament and disposition of the pores that strongly recalls the corresponding features in many *Holectypoida*. In this case, however, regression towards the characters of the ancestral Diademoid ambulacrum would probably produce a comparable effect, so that Clypeus, considered alone, does not afford very clear evidence as to the relation between the *Holectypoida* and Galeropygus.

In connection with these arguments, a strange, but very commonly found detail in the construction of the ambulacra of Galeropygus, deserves mention. At a point about midway between the ambitus and the apical plate of the hypophyllode, a solitary demi-plate is often present. It is in areas I and V that this occurrence is most frequent, and in columns I*a* and V*b* the reduction of the demi-plate is most complete. There is no associated change in the position of the pore-pairs, and the feature appears, in the light of present knowledge, to be a purely gratuitous introduction of complexity. It will be noticed that a comparable development of demi-plates occurs distally in the hypophyllode of *Nucleolites scutatus* (Plate 68, fig. 3), but in that case it is clearly associated with the adoral specialisation. The demi-plates of Galeropygus would excite no surprise if they were only occasionally present as trifling imperfections of plating; but their frequent appearance, and symmetrical distribution, seem to indicate that they introduce a real problem for solution. As to the nature of that solution, I am unable to express an opinion.

(ii) The only group of Irregular Echinoidea which is incontestably related in phylogeny to the *Holectypoida* is that of the Clypeastroida. But there are two other great series of forms, the Spatangoida and the "Cassiduloida," which show ambulacral characters that can be compared with those developed in the *Holectypoida*. The following note on the use of the ordinal terms mentioned is necessary, although the questions involved cannot be discussed in detail. In DUNCAN'S classification (followed by SLADEN and JACKSON in both editions of the American translation of ZITTEL), the term Cassiduloidea was employed, as a sub-section of the Spatangoida, to include all those non-Holectypoid Irregular Echinoids that are neither Echinocorythidæ, Clypeastroids, nor "Heart-Urchins." Under this heading, the groups which contain Conulus, Pyrina, and Amblypygus were comprised. These

forms are here transferred to the Holectypoida. The remainder of the sub-Order was composed of the "Echinobrissinæ," Cassidulidæ, and Collyritidæ. GREGORY (1900) included in the sub-order Asternata much the same series of forms, with the exception of the Conulus-group and the Collyritidæ, which were relegated to the Holectypina and Sternata respectively. Deleting those genera that are here classed with the *Holectypoida*, GREGORY'S two families of Echinonëidæ and Nucleolitidæ, with the addition of the sub-family Clypeina [e] of the Cassidulidæ, comprise most of the Jurassic and Lower Cretaceous non-Holectypoid genera, while the remainder of his Cassidulidæ includes Upper Cretaceous and Tertiary types. The former group is, I believe, entirely distinct from the latter in phylogeny, as in many important points of morphology, and I propose that the two sections should be styled "Nucleolitoida" and "Cassiduloida" respectively. (The Collyritidæ would probably constitute an aberrant family of the former order.) The name Spatangoida is here restricted to those families (except the Collyritidæ) which GREGORY classed as "Atelostomata Sternata." The classification proposed may be summarised as follows, the family names being kept, as far as possible, in agreement with those applied by GREGORY :—

| | |
|---|---|
| Order : NUCLEOLITOIDA . . . | Nucleolitidæ. |
| | Clypeidæ. |
| | Catopygidæ. |
| | Collyritidæ. |
| Order : CASSIDULOIDA . . . . | Cassidulidæ. |
| | Echinolampidæ. |
| | Eolampidæ. |
| Order : SPATANGOIDA . . . . | Echinocorythidæ. |
| | Spatangidæ. |
| | Palæostomidæ. |
| | Pourtalesiidæ. |

These three orders are all characterised by the presence of some degree of petaloid structure in their ambulacra. In the Nucleolitoida, the leaf-like appearance of those parts of the areas is due to a real dissimilarity of the pores. This feature is shown in an extreme degree in Clypeus (Plate 68, fig. 6), where the outer pores are in the form of elongated slits, and the inner ones small and round. In a rudimentary condition, this character is met with in Galeropygus and Plesiechinus, and it is almost obsolete in the Collyritidæ. In the Cassiduloida and Spatangoida, the petals are usually more restricted in extent than in the older order, and derive their appearance from a wide separation of the pores, with or without a superficial groove connecting the pores of a pair. The pores are practically similar, and often differ from those of the extra-petaloid regions merely in their greater separation and size (see Plate 69, fig. 1). Most of the Clypeastroida have pores of this quality, so that

the slit-like pores of the Nucleolitoida seem to be almost restricted to Mesozoic Echinoids, and to have attained their fullest development (in such genera as Clypeus and Pygurus) in the Oolitic period.

(iii) It will be most convenient, in returning to morphological arguments after the foregoing systematic digression, to consider the relation between the Holectypoid ambulacrum and that of the Spatangoida, before discussing the Cassiduloida.

The Spatangid ambulacrum is typically composed of primaries throughout, and these are mostly of a Bothriocidaroid type (with very reduced pore-pairs), except in the petals and peristomial regions. Not infrequently occasional demi-plates may occur in the petals, especially when these are curved (see Plate 69, figs. 1 and 2); and, in some cases, more or less elaborate secondary complication may be developed in the anterior ambulacrum (Plate 69, figs. 2–5). The morphogenetic position of such ambulacra has been discussed in Part I, Sections 1 (c) and 2 (e). There is never, so far as I am aware, any definitely triserial structure either in normal or specialised areas in this order. Since the Spatangoida do not appear before the uppermost Jurassic stages, it seems an inevitable supposition that they must be phylogenetically descended from either the *Holectypoida* or the Nucleolitoida. Their independent origin from any Regular stock is rendered improbable by the definite progress in an exactly opposite direction that had been made by the Diademoida by that time. As regards the ambulacra, there is a far closer apparent accord between the Nucleolitoida and the Spatangoida than between the latter and the *Holectypoida*, but in neither case is there much approximation. The Nucleolitoida have petals, but these are constructed on a different plan from those of the Spatangoida; it is more possible to compare the adapical pores of Pileus with those of a Spatangid petal than those of a Nucleolitid. The Spatangoida have specially constructed regions around the peristome, recalling in position, and probably agreeing in function with, the phyllodes of the Nucleolitoida, but there is no trace of phyllodal plating-structure. The orad plates of the Spatangid ambulacrum are only less Bothriocidaroid than those of the ambitus. Both orders have "biporous" ambulacrals, and this may possibly prove to be a feature that really unites them in spite of the great differences in other respects. But the Echinonëidæ seem to show a stage in what may be regarded as a secondary method of the production of this character.

There is one morphological feature in the ambulacra of the later Pygasteridæ which may possibly serve to link the simplified Spatangid plating with the inevitably more complex structures that preceded it. Pygaster itself shows an almost perfect abandonment of plate-complexity towards the peristome (Plate 65, figs. 3 and 4), and there is reason to believe that the Cretaceous genera Macropygus and Anorthopygus were even more completely simple in this respect. This may seem a very small point of resemblance, and insufficient to serve as a basis for morphogenetic or phylogenetic argument; but the fact remains that the later

Pygasteridæ are the only Echinoids of the Upper Jurassic and Lower Cretaceous periods in which a tendency to ambulacral simplification is seen. The Collyritidæ apparently achieved a similar result in Bajocian times. The correspondence in the structure of the apical system of Anorthopygus and that of the Spatangoida (see HAWKINS, 1912, *a*), adds considerably to the bulk of the evidence that makes reasonable the tentative suggestion that there may be a tendency towards the Spatangoid type in the simplification of the Pygasterid ambulacrum.

(iv) There is more evidence for the formulation of an hypothesis as to the morphogenetic relations between Holectypoid and Cassiduloid ambulacra. Were it not for the Pyrinid nature of its ambulacral plating, Amblypygus would naturally be classed as a primitive Echinolampid with rudimentary phyllodes. If Amblypygus had no petals, it would almost inevitably be included among the Conulinæ. Further, Conulus has a strongly triserial arrangement of pore-pairs around the peristome which could be modified into a true phyllode by trifling addition to the complication already present in the plates. By slight modifications in the nature of the pore-pairs, and by a gradual simplification of the ambulacral plating (two morphogenetic processes that certainly occurred during the evolution of the *Holectypoida* themselves), the ambulacrum of the Echinonëidæ could readily have given rise to that of the Cassiduloida. Amblypygus seems to show the modification of the apicad pores, while Conulus has structures preliminary to the modification of the orad pores. All that is needed to complete the history of the transformation is a case in which the plating is in process of simplification. That such evidence will be found in Cretaceous or Lower Tertiary Cassiduloida I am confident. In spite of the superficial resemblance between many of the Cassiduloida and Nucleolitoida, in both ambulacral and other structures, there seems reason to believe that it must be ascribed to the principle of heterogenetic homœomorphy. If the suggestions as to the qualities of Micropetalon, given in Section 1 of this part of the paper, should prove to be correct, that small form would serve as an ontogenetic support to the belief in the derivation of the Cassiduloida through the Echinonëidæ.

(v) It is but rarely that such relative certainty as to the phyletic connection between two orders can be found as that which, by universal consent, obtains in the case of the *Holectypoida* and Clypeastroida. The actual family from which the latter group arose is definitely indicated. GREGORY (1900) emphasized this transition in correcting the indefensible generic term "Echinites" of DUNCAN into the suggestive name of "Protocyamus." His correction was no more legitimate than the original name, since *Discoidea subucula*, the type of the proposed genus, is already the type of Discoidea. But the significance of the name stands. The characters of the apical system alone are sufficient to bind the Discoidiidæ very closely to the Clypeastroida, but there is abundant confirmatory evidence.

Nevertheless, in the matter which concerns the present work, there is a discordance in ambulacral structure in the two groups that, at first sight, seems

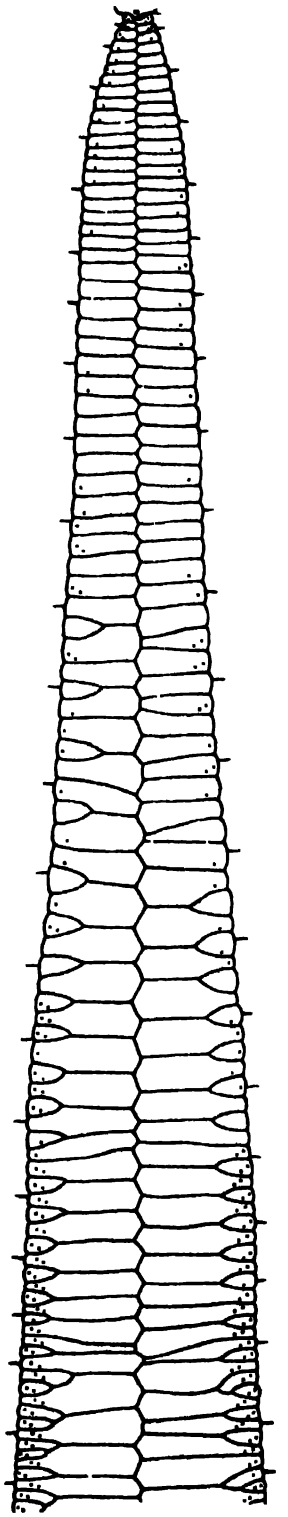
almost sufficient to outweigh the many similarities. Between the intensely complex ambulacral plating of the larger Discoidiidæ and the "Bothriocidaroid" ambulacrals Clypeaster, and between the minute apicad pores of the Cretaceous family and the highly developed petals of the Tertiary group, a great gulf seems to exist. When to these differences is added the anomalous distribution of the non-petaloid pores of the Clypeastroids, scattered as they are over ambulacral and interambulacral plates in defiance of the rules governing the structure of all other Echinoids, it is seen that there is a serious morphogenetic problem if the phylogenetic sequence is to be upheld. It is with surprise, not unmixed with satisfaction, that I have been able to trace the connection between the Discoidiid and Clypeastroid ambulacra in such detail that the morphogenetic relationship between the two sets of structures would need to be postulated even without the support of arguments based on other features.

The modifications of ambulacral structure found among the Clypeastroida are capable of reference to three types. The first, which may be termed Fibulariid, shows short and not very marked petals containing large, similar pores set in distant series owing to the considerable height of the plates; and more or less "Bothriocidaroid" other parts, in which each plate is perforated by numerous minute pores, either arranged in transverse linear series near the apicad margin, or occurring in congested groups. The podial pores seem to be restricted to the ambulacral areas. The remaining two types, Scutellid and Clypeastrid, resemble one another (and differ from the Fibulariid) in the great elaboration of the petals, the typically "Bothriocidaroid" shape of the other ambulacrals, and the dissipation of the extra-petaloid pores over the interambulacral areas. The Scutellid type has petals composed of very great numbers of excessively slender primaries; in the Clypeastrid type the corresponding plates are of greater height, and are arranged on the plan of alternating primaries and demi-plates (see Plate 68, fig. 7). In all three types there are two features that are constant in character though not in quality. The pores of the petals are very nearly similar, the petaloid effect being attained by the wide separation of the individuals of a pair, and the occurrence of a well-marked superficial groove passing from one to the other along the transverse suture. The extra-petaloid pores are exceedingly minute (rarely visible except in stained or sectioned specimens), and are unlike those of any other series of Echinoids in their departure from the "one plate, one pore-pair" principle of distribution.

The Fibulariid and Scutellid types are alike in the simplicity of their plating, and the latter is clearly the morphogenetic outcome of intensification of the tendencies present in the former. In plating-structure, the Clypeastrid ambulacrum is almost unique, and the regular alternation of primaries and single demi-plates is very different from any familiar types of ambulacral complexity. Both Fibulariid and Clypeastrid types occur in the Lower Eocene, if not in the Upper Cretaceous;

the Scutellid type is slightly later in appearance. It is, therefore, necessary to seek for morphological "ancestors" for the first two types only. The extreme difference between the sparsely plated ambulacra of Fibularia and the crowded and complex petals of Clypeaster makes it difficult to believe that these two types could have arisen at one and the same time from a common ancestral type; although, in default of evidence to the contrary, such a suggestion might be made.

In the Discoidiidæ there are two well-marked types of ambulacral structure, which appear to show divergent morphogenetic trends. On the one hand, the small forms typified by *D. subucula*, and succeeded by *D. dixoni*, have relatively simple ambulacra with a tendency to the development of increasing simplicity adapically, and increasing complication adorally. *D. dixoni* (Plate 67, fig. 2) has high apicad ambulacrals, and Pyrinid ambital and adoral plates. The shape and proportions of the apicad plates are very closely analogous with those of Fibularia. But the complex triad-grouping of the rest of the ambulacrum of *D. dixoni* is (or appears to be) in violent contrast to the "Bothriocidaroid" plating of the corresponding regions of all Clypeastroids. None the less, I am convinced that the contrast is more apparent than real, but the reasons for this belief will be better indicated in a discussion of the other Discoidiid type in its relations to the Clypeastrid. In *D. cylindrica* (Plate 66) the apicad plates seem to retain more or less "Cidaroid" proportions. while those at and below the ambitus possess complexity and congestion of a remarkable kind. In high-zonal forms, and especially in gerontic individuals, a considerable sequence of the plates of the adapical surface assumes the plan of alternate primaries and demi-plates. The fine specimen (58·2 mm. in diameter, 41·9 mm. in height, collected by G. E. Dibley, Esq., from the zone of *H. subglobosus* at Oxted) from which the accompanying text-fig. 3 is taken, is the largest example of the species that I have seen. (The original of Plate 66, fig. 1, has a diameter of 57 mm.) It also shows the longest continuous series of alternate primaries and demi-plates that I have detected, although there is an almost complete absence of the sporadic precocious apicad complexity that is usual in large specimens from this horizon. It is a striking fact, and one that must surely



Text-fig. 3.—Ambulacrum V of a gerontic specimen of *Discoidea cylindrica*, from the apex to the ambitus, showing the great development of "Clypeastrid" primaries and demi-plates.

have great morphological significance, that such a type of structure is absolutely restricted to the adoral surface of the later members of this species and the petals of the Clypeastridæ. The similar plating of some parts of the petals of *Heteraster oblongus* (Plate 69, fig. 2) is hardly comparable, since in that case it is clearly an adaptation towards the accommodation of more plates in one column of the area than in the other.

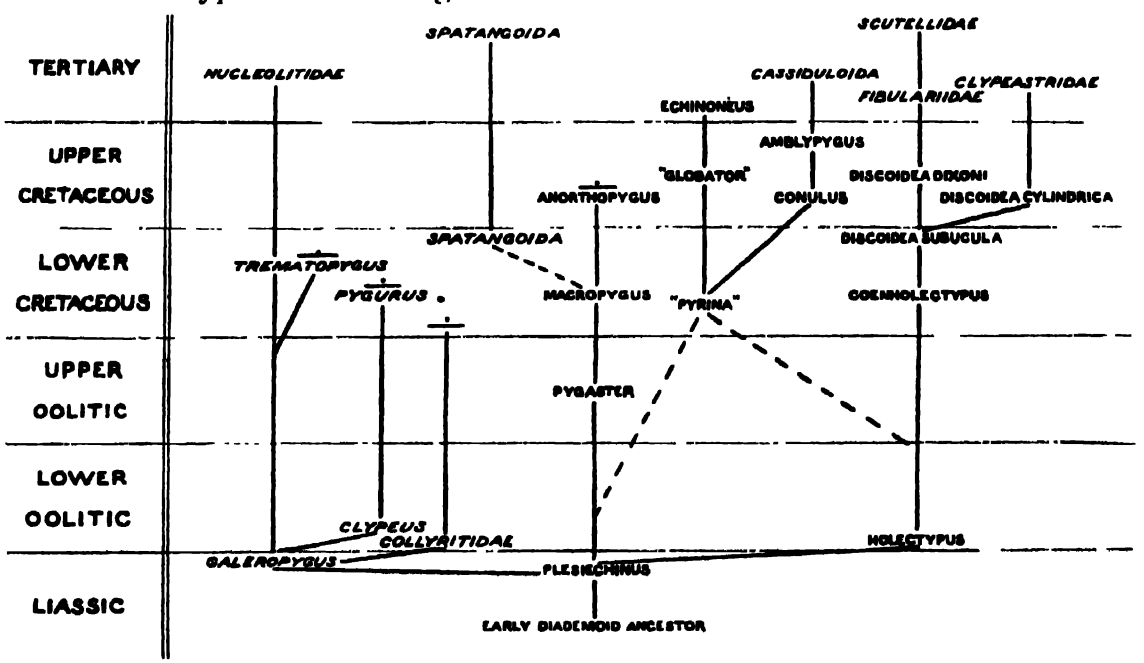
As far as the plating of the apicad parts of the ambulacra is concerned, it thus appears that there is a tendency towards the Fibulariid type shown in the *D. subucula* series, and an equally marked tendency towards the Clypeastrid type in the *D. cylindrica* series. In both lineages of the Discoidiidæ there is a progressive increase in the complication of the adoral parts of the ambulacra, while in both Clypeastroid groups plate-simplicity seems to be present in its ultimate phase. It must, however, be borne in mind that the simplification of the extrapetaloid parts of Clypeastroid ambulacra is more apparent than real, for the number of podia is greatly in excess of that of the plates, and their distribution is extraordinary.

The congestion of the ambital ambulacrals in *D. cylindrica* is such that the pore-pairs (which are very minute) are compelled to take on an irregularly multiserial disposition, and even so are scarcely to be accommodated within the plates to which they belong. Many of the demi-plates of that region are so small that they are definitely inadequate to contain the peripodia. It may be presumed that the need for, or tendency towards, the production of great numbers of podia has resulted in the exertion of "growth-pressure" on the plates involved. In Part I, Section 2 (*d*) (p. 410), it has been shown that when comparable excessive pressure has been exerted on the ambulacrals of *Echinus esculentus* (as a teratological feature), there is a tendency towards the complete destruction of the demi-plates, and the ejection of their pore-pairs into the adjacent interambulacra. The degree of compression and reduction in the areas of the specimen of Echinus there described is moderate in comparison with that normally developed in *D. cylindrica*. If the principle of plate-complexity stated on p. 407 is sound, and ambulacral plates can be destroyed by excessive compression and consequent reduction, then it must be admitted that two-thirds of the ambulacrals of the ambital region in *D. cylindrica* are in imminent danger of obliteration. On their resorption the podia would need to pass through the test in some neighbouring part, while the removal of the limiting plates with which they were originally associated would enable them to spread unchecked over as wide a region as was compatible with the exercise of their function. Further, the nature of the plating of the adoral parts of the ambulacra in *D. cylindrica* is such that the primary plates would show characteristic "Bothriocidaroid" proportions if the minute demi-plates were destroyed.

The number of minute, dissipated pores that perforate a Clypeastrid corona is very great; and, whether they are in pairs or not (a question to which I have been unable

to find a reliable answer), is in excess of the proportionate numbers of pore-pairs in the Discoidiid ambulacrum. But since podia are produced by "budding" from the radial canal, and those of Clypeastroids are, in many cases, developed from branches of that vessel rather than from the main trunk, there seems no logical limit to the rate of their increase when once the rule of association with separate plates has been broken. Although at the outset it would have seemed rash, if not utterly speculative, to suggest that the complex areas of *D. cylindrica* are the direct morphological predecessors of the apparently simple areas of Clypeaster, the various tendencies of ambulacral development that have been indicated throughout the paper all seem to make such a suggestion not only reasonable but inevitable.

It is unlikely that ontogenetic study of recent types of the Clypeastroida would make it possible actually to trace the destruction of the Discoidiid ambulacrals. When once simplicity of plating had been acquired in morphogeny, ontogenetic acceleration would speedily tend to drop the vestigial production of the demi-plates, and the only indication of the previous existence of such structures would appear in the great numbers of podia in proportion to the plates. This indication is maintained in all Clypeastroids throughout life.




TEXT-FIG. 4.—Table showing the relation of the ambulacral structure of the *Holectypoida* with that of the other irregular orders. When generic names are used, the genera are intended to serve as types of structure, and no necessary phyletic association is involved. A transverse line with a dot above indicates the termination of a morphogenetic series

The ambulacra of the Clypeastroida thus seem to have a double morphogenetic origin. The Fibulariid type can be traced back to the later members of the *Discoidea subucula*-series, while the Clypeastrid type has its forerunner in

*D. cylindrica*. Again, the petaloid parts of the Clypeastroid types are structurally simple, although a peculiar type of restrained complexity occurs in those of the Clypeastridæ; but the extra-petaloid parts have been simplified (as regards plating) by the somewhat heroic method of the destruction of most of their constituent plates, and the scattering of their pores. The attainment of the "Bothriocidaroid" stage of reversion in Spatangid ambulacra has involved a corresponding reduction in the numbers of podia; it is doubtful whether the comparison of the high, hexagonal ambulacrals of Clypeaster with those of Bothriocidaris is justifiable. So far from showing true reversionary simplification, the ambulacra of the Clypeastroida represent an ultimate phase of plate-complexity, which gives a deceptive appearance of simplicity.

This section, and the whole paper, can be best closed by an attempt to express the conclusions reached in the form of a morphogenetic table (text-fig. 4).

It is at least probable that many of the connecting lines in the "tree" have a real phylogenetic meaning; but it is unlikely that lines of descent calculated from a single series of data will in all cases coincide with the true course of phyletic evolution. In spite of the many uncertainties involved in the diagram, one point seems clearly brought out. The *Holectypoida* are an annectant group in the most literal sense of the expression. Since their origin from a Diademoid stock, they have given rise, at different periods and by different directions of modification, to all the orders of the Irregular Echinoidea.

## 4. Summary.

The form of this summary is that of a "catalogue raisonnée" of the various sections of the paper. It is hoped that the amplified "list of contents" thus provided will enable those who are interested in any particular point raised to refer directly to the section in which it is discussed.

Part I.—Section 1 (*a*) The classification of the Regular Echinoids that has proved most satisfactory in the work is that given by Gregory (1900).

(*b*) The ambulacrum of Bothriocidaris is believed to represent the most primitive type. The early ontogenetic stages of many Recent forms seem to possess such areas, and the later Irregular Echinoids revert to a similar structure in the parts of their ambulacra that have become degenerate in function.

(*c*) The trend of evolution of the ambulacrum in the early and Regular Echinoids was two-fold. The number of podia (*i.e.*, plates) was more or less steadily increased from their scarcity in Bothriocidaris, and the plating-structure had consequently to be adjusted to allow of multiplication without the development of coronal fragility. In the "Perischoechinoida" there were two distinct lines of ambulacral morphogenesis—the "Palæechinoid," in which the plates retained their disposition in two columns and became much lowered, and the "Melonechinoid," in which "klasma-plating" produced multicolumnar areas, suited to the requirements of flexible tests, but impracticable

for rigid ones. By a flexing of the areas, the Palæechinoid type became modified into the "Archæocidaroid" type, which is essentially like the true Cidaroid type of later periods. Klasma plates are believed to be essentially similar to the reduced plates of elaborate Euechinoid ambulacra, and to have assumed their peculiar arrangement under the same influences that produce a like distribution of the ambulacrals of the Echinothuriidæ. Attention is drawn to the remarkable similarity between the simpler klasma-plating of some Palæozoic Echinoids and the secondary complexity that occurs in area III of *Echinocardium cordatum*. It is suggested that the latter development marks a reversionary tendency in the Spatangidæ no less than the "Bothriocidaroid" nature of the obsolete ambulacrals of that family.

(*d*) The Cidaroid type of ambulacrum represents the best obtainable result, as regards mechanical strength, when the plates are multiplied but not specially modified. All Euechinoid ambulacra can be traced back to this stage of development, unless they are so reversionary that they exhibit only Bothriocidaroid plating. Incipient complexity is found in the strongly curved ambulacra of Paracidaris, and incipient diversity of ornament and size (almost amounting to grouping) occurs in the Diplocidaridæ.

(*e*) i. Typical Saleniidæ have "dyad-groups" (which may become dyad-compounds adorally) almost throughout the area, thus showing but a small morphogenetic advance on the Diplocidarid condition. The Acrosaleniid ambulacrum shows a further stage in complexity; simple, uncombined plates occur between the dyads, and usually unite with them to form triads below the ambitus.

ii. The Diademina show "Acrosaleniid" triads in typical cases, but these compounds (or groups) often tend towards an "Arbacioid" structure. In several forms two triads may become united to form hexad "super-compounds." In many Upper Jurassic types extra demi-plates are added within the compounds, and this condition becomes normal and regular in the Cretaceous Phymosomatidæ.

iii. The Arbacina have typically "Arbacioid" triads, but these are liable to modification by the same two processes that affect the Diademoid compounds from which they are believed to be derived. The compounds may be elaborated by the addition of extra plates to their apicad margins, as an alternative to the incorporation of interstitial demi-plates.

iv. The Echinina with "Echinoid" triads show a remarkable constancy of structure, although tendencies to the production of "super-compounds" occur. In the Strongylocentrotidæ and Echinometridæ the incorporation of interstitial demi-plates is progressively carried to a high degree of elaboration. The many plated multiporous compounds of Heterocentrotus have Bothriocidaroid proportions and relations, more than Bothriocidaroid strength, and include a vastly greater number of podia; they represent the successful solution of the problem of podial multiplication without coronal weakness.

Section 2 (*a*) Slight additions and modifications are made in the terminology applied to ambulacral structures.

(*b*) A distinction is drawn between "grouped" and "combined" plates. The former phase of complexity is preliminary to the latter; it is characterised by the maintenance of the transverse sutures of the plates without reduction of sutural tissue. The controversy as to the cause of the production of compound plates is considered, and the conclusion is reached that while the *reduction* of plates is to be ascribed to "growth-pressure" (DUNCAN) of various kinds, *combination* is almost always dependent originally upon the growth of large tubercles (LAMBERT), which serve to bind the components together. While "combination" is progressively intensified in the Regular Echinoidea, it is believed to be absent from the Irregular forms, where "grouping" (often very elaborate in character) represents the highest degree of complexity attained.

(*c*) The first phase of plate-complexity is marked by a grouping of previously simple primaries into dyads, followed by their combination. Subsequently (or perhaps before combination is complete), alternate simple plates appear between the dyads, and these gradually unite with the dyads adoral to them, forming Diademoid triads. More elaborate compounds (or groups) may be produced by a repetition of this process (*e.g.*, Arbacia), or by the intercalation of extra plates (usually reduced) within the compounds (*e.g.*, Phymosoma or Heterocentrotus).

(*d*) The production of demi-plates is ascribed to an attempt to reduce the quantity of sutural tissue in a compound rather than to actual compression. On the other hand, occluded and included plates appear to result from the operation of "growth-pressure." A detailed analysis of certain abnormal developments in the ambulacra of Echinus shows (i) that sutures can be obliterated by intense "crushing"; (ii) that plates may become gradually resorbed under the influence of the same force, their podia either undergoing atrophy or being driven into the interambulacra; and (iii) that in so stereotyped a style of structure as the "Echinoid," plates that are introduced between the compounds suffer reduction and ultimate resorption, while those introduced into a compound may be incorporated to form permanent tetrads like those of Strongylocentrotus. A similar analysis of the ambulacrum of a gerontic Heterocentrotus seems to indicate that the high, complex compounds of this form are really super-compounds of a Strongylocentrotid pattern, increased and modified.

(*e*) It is shown that, in the Regular Echinoids, plate-complexity is always present in those forms which have strongly adhesive podia, and that the two conditions seem to vary in direct proportion. Complication in the ambulacra of the Irregular Echinoids is always associated with those parts of the areas that possess important functional value. According to the distribution of utility, the rate of production of plates may vary in the different areas (*e.g.*, *Echinocardium cordatum*), or even in the separate columns of one area (*e.g.*, *Heteraster oblongus*). Ambulacral complication in

the Irregular forms seems never to result in combination, and usually produces structures closely similar to those of the simpler Palæozoic types.

(*f*) It is argued that JACKSON'S principle of "localised stages of development" has only a partial application to ambulacra of post-Palæozoic Echinoids. The ontogenetically early plates may become much modified by pressure, and so lose their originally simple character. However, in the actual composition of compound plates the principle seems to hold good. In the Irregular Echinoids the principle fails almost completely to account for the observed structures. The apicad plates of a Spatangid petal are in a far higher state of development than those of the mid-zone, and the orad-plates of a Cassiduloid phyllode are even more complex, though ontogenetically young. In these forms, "localised function" is the determining factor in the morphogeny of ambulacrals.

Part II.—Section 1. Detailed descriptions of the ambulacra of representative genera and species of the *Holectypoida* are given. There are four main types of structure in the order. The "Plesiechinid" type has "Acrosaleniid" triad-groups adorally, with some more or less irregular grouping in the region of maximum tuberculation. This type occurs in Plesiechinus, the Holectypidæ, and *Discoidea subuculа*. The "Pygasterid" type has completely simple structure (save for ornament and ambital "tubercle-grouping"). It occurs only in the later Pygasteridæ. The "Pyrinid" type recalls the "Echinoid" triads of many Regular Echinoids, and has triad-groups (with one demi-plate) almost throughout the area. It occurs in an incomplete phase in *Discoidea dixoni*, and in full development in the Lanieriidæ and the Echinoneidæ, including Amblypygus. The "Discoidiid" type is confined to the series of forms specifically united as *D. cylindrica*. It shows extreme "triad" complexity adorally (usually carried out with marked irregularity), and, in gerontic forms from high zones, a tendency to the development of alternate primaries and demi-plates on the adapical surface.

Section 2. In the Jurassic Pygasteridæ feeble attempts at the development of petals were made, but they were abandoned by the Cretaceous members of the family, and do not occur in the other families. It is considered doubtful, however, that the Holectypoid podia could exert a strong adhesive power, in view of the practically uniserial arrangement of the pores and absence of plate-combination. The congestion of pores near the ambitus is believed to indicate the concentration of podial functions to that region, and these functions would be largely sensory, especially in Cretaceous forms which lived on loose sand or ooze. It is suggested that the extremely crowded, and strongly convergent, filamentous podia of the adoral parts of the Discoidiid ambulacra may have served to pass food-particles from the ambitus to the mouth. The Pyrinid podia are known to have some slight adhesive powers, but these are chiefly employed in holding small objects as a protective cover for the test.

Section 3. i. The Plesiechinid type of ambulacral structure is regarded as primitive for the order. By a steady simplification the Pygasterid type must have

evolved from it. The Pyrinid type can be seen to develop from the Plesiechinid in such a sequence as that of *Discoidea subuculа* and *D. dixoni*, but is not likely to have been derived through those species. The Discoidiid type is evidently an elaboration of an incomplete Pyrinid type, and its extreme variability in detail (a feature strongly contrasting with the general characters of Echinoid ambulacra, however elaborate), is believed to indicate morphogenetic instability preceding fresh modification.

ii. The Plesiechinid type is almost identical in essential characters with the structure shown in Acrosalenia, and marks an intermediate stage between the formation of dyads and that of triads. Such a morphogenetic phase will have been general among Liassic (especially Lower Liassic) Diademoida; so that, on ambulacral evidence alone, the origin of the Holectypoid ambulacrum can only be definitely traced to an early Diademoid form.

iii. A new classification of the non-Holectypoid Irregular Echinoids is proposed. While the ambulacra of Galeropygus (the earliest Nucleolitoid) might well have arisen from Diademoid types independently of the Holectypoida, the characters shown by later modifications in the order (especially by Trematopygus) are believed to indicate that the Nucleolitoid line of evolution branched from that of Plesiechinus. There is little evidence as to the relation of the Holectypoid ambulacrum with that of the Spatangoida (*sens. str.*), but it is noteworthy that the later Pygasteridæ, alone of Upper Jurassic Echinoids, show that progressive simplification of ambulacral plating which must have preceded the development of the Spatangid ambulacrum. The Cassiduloid ambulacrum is believed to be traceable to that of Conulus (nearly through that of Amblypygus), and the hope is expressed that stages in simplification of plating will be found in Eocene forms. Micropetalon is believed to be an early ontogenetic stage of some Cassiduloid, showing mainly Echinonëid features. The Clypeastroida show two distinct types of ambulacra, the Fibulariid (leading to the Scutellid) and the Clypeastrid. The former is directly foreshadowed in the later species of the small Discoidiidæ, while the latter is clearly derived from the Discoidiid ambulacrum. The anomalous scattering of the podial pores in the Clypeastroida is ascribed to the destruction of their containing plates by an over-development of "plate-complexity," and the apparently "Bothriocidaroid" ambulacrals of their adoral surfaces are thus not analogous with the similar plates in other Irregular groups. While in all other Irregular Orders the evolution of the ambulacra has been in the main reversionary, in the series Plesiechinus—Discoidea—Clypeastroida, it has followed lines similar in many respects to those normally taken in the Diademoida. While Heterocentrotus shows the culmination of plate-complexity with combination, Clypeaster represents the acme of plate-complexity without combination carried to the ultimate phase of plate-destruction.

## 5. References to Publications Quoted.

The following list does not include a tithe of the papers and books which have been utilized in the course of the work. But it would have entailed the construction of a catalogue of unwieldy length and of little value, had the titles of all the papers that have been consulted been incorporated. Only those publications, to which specific reference is made in the preceding pages, are catalogued here :—

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(29) LAMBERT, J., and THIÈRY, P., 1908. "Révision des Échinides jurassiques du Département de la Haute-Marne," 'Bull. Soc. Nat. Haute-Marne, Année 5, No. 20, pp. 1–32, Plate 4. [Correct pagination unknown.]

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(31) LOVÉN, S., 1875. "Études sur les Échinoidées," 'K. Svensk. Vet.-Akad. Handl.' Band 11, No. 7.

(32) *Idem*, 1888. "On a Recent Form of the Echinoconidæ," 'Bihang K. Svensk. Vet.-Akad. Handl.,' Band 13, Afd. 4, No. 10.

(33) *Idem*, 1892. "Echinologica," 'Bihang K. Svensk. Vet.-Akad. Handl.,' Band 18, Afd. 4, No. 1.

(34) Noetling, F., 1897. "Fauna of Baluchistan," vol. 1, Part 3. "Fauna of the Upper Cretaceous (Maëstrichtien) Beds of the Mari Hills," 'Pal. Indica,' ser. 16, pp. 1–79, Plates 1–23.

(35) Pomel, A., 1883. "Classification Méthodique et genera des Échinides vivants et fossiles," Alger.

(36) Spath, L. F., 1919. "Notes on Ammonites," 'Geol. Mag.,' Dec. 6, vol. 6, pp. 27–35.

(37) Thiéry, P., 1911. "Notes sur quelques Échinides," 'Bul. Soc. Hist. Nat.,' Haute-Marne, Tome (?) 1, pp. [1–7 ?], Plate 1.

(38) Westergren, A. M., 1911. "*Echinoneus* and *Micropetalon*," 'Mem. Mus. Comp. Zool.,' Harvard, Sci. Res. "Albatross," vol. 15, pp. 41–68, Plates 1–31.

## 6. EXPLANATION OF PLATES 61–69.

All the figures have been drawn by the author. The lack of artistic merit that may result from this is compensated by the accuracy with which the structures are indicated. The tracing of sutures, particularly in fossil Echinoids, is a faculty that can be acquired only by long experience, and to the uninitiated is full of pitfalls and uncertainties. An attempt has been made to arrange the figures in such an order that they afford a pictorial record of the stages of specialization in the ambulacra of the Echinoidea. Most of the drawings are considerably magnified, but the actual degree of enlargement is immaterial in the majority of cases. Where it has any significance, the magnification can be ascertained by reference to the text. Those figures that are copied from other works are not necessarily identical with their originals in every detail, but are faithful reproductions of the parts with which the present paper is concerned.

### Plate 61.

Fig. 1.—Ambulacrum III of *Bothriocidaris archaica* (from Jackson, 1912, Plate 1, fig. 1, *pars*). This figure includes the peristomial ambulacrals, which are not clearly separable from those of the corona.

Fig. 2.—Ambulacrum III of a very young *Goniocidaris canaliculata* (adapted from Lovén, 1892, Plate 2, figs. 7, 8 and 9).

Fig. 3.—Ambulacrum III of young *Mellita hexapora* (modified from Lovén, 1875, Plate 49, fig. 241, *pars*).

Fig. 4.—Ambulacrum III of very young *Brissopsis lyrifera* (from Lovén, 1875, Plate 37, fig. 218, *pars*).

Fig. 5.—Ambulacrum III of *Echinocorys sulcatus* (from Lovén, 1875, Plate 24, fig. 181, *pars*).

Fig. 6.—Ambulacrum III of *Spatangus purpureus* (from Lovén, 1875, Plate 36, fig. 208, *pars*).

Fig. 7.—Ambulacrum of *Palæechinus quadriserialis* (modified from JACKSON, 1912, Plate 30, fig. 3, *pars*).

Fig. 8.—Ambulacrum of *Hyattechinus beecheri* (modified from JACKSON, 1912, Plate 26, fig. 1, *pars*).

Fig. 9.—Part of ambulacrum of *Maccoya burlingtonensis* (from JACKSON, 1912, Plate 33, fig. 2, *pars*).

Fig. 10.—Adapical part of ambulacrum of *Lovenechinus missouriensis* (from JACKSON, 1912, Plate 42, fig. 3).

Fig. 11.—Internal view of adoral part of ambulacrum of the same species (from JACKSON, 1912, Plate 42, fig. 5).

Fig. 12.—Adapical part of ambulacrum III of *Lepidesthes colleti* (from JACKSON, 1912, Plate 71, fig. 1, *pars*).

Fig. 13.—Detail of ambulacrum of *Lovenechinus* near mid-zone (from JACKSON, 1912, Plate 42, fig. 2).

Fig. 14.—Part of ambulacrum of *Archæocidaris rossica* (from JACKSON, 1912, Plate 12, fig. 9).

Fig. 15.—Part of ambulacrum of *Lepidocidaris squamosa* near mid-zone (from JACKSON, 1912, Plate 17, fig. 12).

Fig. 16.—Part of ambulacrum of the same species, near mid-zone (from JACKSON, 1912, Plate 17, fig. 3).

## PLATE 62.

Fig. 1.—Part of ambulacrum (between the ambitus and the ocular plate) of *Paracidaris florigemma* (Univ. Coll., Reading, No. 23). Showing the intercalated plates on the convex columns adapically, where the curvature is sharp.

Fig. 2.—Part of ambulacrum of *Diplocidaris verrucosa* (from DE LORIOL, 1890, Plate 8, fig. 27A). The perradial suture is probably incorrectly drawn.)

Fig. 3.—Ambulacrum of *Salenia texana* (from CLARK and TWITCHELL, 1915, Plate 12, fig. 1F).

Fig. 4.—Ambulacrum of *Acrosalenia* (generalized from several species, and from THIERY, 1911. Plate 1, fig. 12).

Fig. 5.—Adoral part of ambulacrum of *Orthopsis occidentalis* (from CLARK and TWITCHELL, 1915, Plate 17, fig. 1D, *pars*).

Fig. 6.—Ambulacrum III of *Diplopodia versipora* (Univ. Coll., Reading, No. 519).

Fig. 7.—Ambulacrum III of *Stomechinus bigranularis* (Univ. Coll., Reading, No. 201).

Fig. 8.—A "super-compound" of *Astropyga radiata* (from DUNCAN, 1885, *a*, Plate 5, fig. 9).

Fig. 9.—Internal view of three plates of the same species (from DUNCAN, 1885, *a*, Plate 5, fig. 10).

Fig. 10.—Part of ambulacrum of *Tripneustes proavia*, showing a "super-compound" (from DUNCAN and SLADEN, 1885, *a*, Plate 48, fig. 4, *pars*).

Fig. 11.—Ambulacral plates of *Acrocidaris nobilis* from the mid-zone and adoral surface. The former is a super-compound (from DE LORIOL, 1890, Plate 14, fig. 8).

Fig. 12.—Ambulacral plates from near the mid-zone in *Hemicidaris mondegoensis*. The plates are all primaries, and are grouped, but apparently not combined, into super-compounds (from DE LORIOL, 1890, Plate 13, fig. 12).

Fig. 13.—Ambulacrum III of *Phymosoma koenigi* (Univ. Coll., Reading, No. 653).

Fig. 14.—Part of ambulacrum III (mid-way between ambitus and apex) of *Hemicidaris intermedia* (Univ. Coll., Reading, No. 517).

Fig. 15.—Ambulacrum of *Glyptieus hieroglyphicus* (after LAMBERT and THIÉRY, 1908, fig. 2).

Fig. 16.—Part of ambulacrum of *Leptarbacia argutus* (from CLARK and TWITCHELL, 1915, Plate 16, fig. 1D, *pars*).

## PLATE 63.

Fig. 1.—Ambulacrum of *Tetrapygus niger*, drawn from an etched specimen and partly from thin sections. Adapically uncombined plates separate the "Arbacioid" triads. Towards the ambitus these plates become incorporated into the compounds. Adorally the compounds are tetrads, in the mid-zone typically pentads.

Fig. 2.—Ambulacrum of an adult *Echinus esculentus*, drawn from an etched specimen. Normal "Echinoid" triads throughout.

Fig. 3.—Ambulacrum of *Echinometra lucunter*, drawn from an etched specimen. The orad compounds are apparently triads, followed adapically by tetrads and pentads. These last types persist to the ocular plate. Save in proportions, this figure would equally illustrate the ambulacrum of *Strongylocentrotus*.

Fig. 4.—Part of ambulacrum of *Noetlingia boulei* above the ambitus (modified from LAMBERT, 1906, p. 13, fig. 9).

Fig. 5.—Adoral part of ambulacrum of the same species (modified from LAMBERT, 1906, p. 12, fig. 8).

Fig. 6.—Mid-zone of ambulacrum III of *Echinus esculentus*, 70 mm. in diameter, showing the first phase in the production of super-compounds.

Fig. 7.—Mid-zone of ambulacrum III of another specimen, 105 mm. in diameter. Certain triads have become separated from the perradial suture, being compound-demi-plates and components of super-compounds.

Fig. 8.—Part of ambulacrum IV (mid-way between ocular and ambitus) of abnormal *E. esculentus*. At X additional demi-plates occur between the normal

triads. They are provided with fully-developed sutures, and are in no sense combined with the neighbouring plates. The two in column *b* have slightly reduced pore-pairs.

Fig. 9.—Part of ambulacrum I (mid-way between ocular and ambitus) of the same specimen. At X a similar plate to those found in fig. 8 occurs. At X′ an "attempt" at "Arbacioid" structure appears, but the two demi-plates are not combined with the intervening primary.

Fig. 10.—Three plates from one column of ambulacrum of *E. esculentus*, showing a normal "Echinoid" triad, a regressive "Diademoid" triad, and an "inverted Echinoid" triad. The plates are drawn disproportionately high for the sake of clearness; they are not otherwise diagrammatic.

Fig. 11.—Part of ambulacrum I (below the ambitus) of the same specimen as that represented in figs. 8 and 9. An intercalated occluded plate (uncombined, and with an obsolescent pore-pair) occurs along the transverse suture separating two normal triads. This is probably a late stage of the abnormalities marked X in figs. 8 and 9. It compares remarkably with *Noetlingia* (figs. 4 and 5).

Fig. 12.—Part of ambulacrum III of a different specimen of *E. esculentus*, at the mid-zone. A surplus triad is in process of obliteration.

Fig. 13.—Part of ambulacrum III of the specimen figured in figs. 8, 9 and 11, midway between ambitus and peristome. At X an intercalated demi-plate makes its compound "Strongylocentrotid." The supernumerary plate is surrounded by reduced sutures, having entered into true combination with its neighbours.

Fig. 14.—Part of ambulacrum IV, from the ambitus adorally, of a large abnormal specimen of *E. esculentus*, in the collection of Ll. Treacher, Esq. For description, see p. 410).

## Plate 64.

Fig. 1.—Adapical part of ambulacrum of a gerontic specimen of *Heterocentrotus mammillatus*.

Fig. 2.—Mid-zone of the same ambulacrum.

Fig. 3.—Adoral part of the same ambulacrum.

Fig. 4.—Part of the surface of the adradial suture of the same area, showing the difference in the arrangement of the plates on the two surfaces of the test.

Fig. 5.—Section of the adoral part of another area from the same specimen, with the plate-boundaries traced between crossed nicols. The dotted circles mark the positions of the tubercles. The pores are somewhat differently placed from their external positions, owing to the obliquity of their passage through the test.

Fig. 6.—Two compounds from the orad part of the ambulacrum of *Colobocentrotus atratus*, drawn from a section viewed between crossed nicols. Slightly diagrammatic.

(For description of all these figures, see p. 412, *et seq.*)

## Plate 65.

Fig. 1.—Plan of ambulacrum IV of *Plesiechinus ornatus*.

Fig. 2.—Detail of adoral parts of ambulacrum IV of *P. ornatus* (Univ. Coll., Reading, No. 120). The X marks the position of the few simple plates that separate the two series of grouped plates. The apicad grouping is influenced by the tubercles; the orad grouping is like that of *Acrosalenia*.

Fig. 3.—Plan of ambulacrum II of *Pygaster semisulcatus* (Univ. Coll., Reading, No. 804).

Fig. 4.—Detail of adoral parts of area I in the same specimen. In the apicad part of the figure "tubercle-grouping" is present, but adorally the plating is like that of *Orthopsis*.

Fig. 5.—Adapical ambulacrals of *Pileus pileus* (from de Loriol, 1890, Plate 21, fig. 1e).

Fig. 6.—Portion of the adapical part of ambulacrum II in *Pygaster macrocyphus* (co-type, Brit. Mus. Coll.), illustrating the type of abnormality commonest in Jurassic Holectypoida.

Fig. 7.—Plan of ambulacrum V of *Holectypus "depressus"* (Cornbrash).

Fig. 8.—Detail of adoral parts of ambulacral IV of *H. hemisphæricus*. The plating is closely similar to that of *Plesiechinus*.

Fig. 9.—Detail of adoral parts of ambulacrum V of a Cornbrash *H. "depressus"* (a different specimen from that shown in fig. 7). The plating, though still Plesiechinid in plan, is remarkable for the great height of the ambulacrals.

## Plate 66.

### *Discoidea cylindrica*.

Fig. 1.—Plan of ambulacrum of a specimen from the "Lower Chalk," Folkestone (Manchester Mus., No. L 7740). Above the ambitus considerable numbers of "Clypeastrid" demi-plates occur, and adapically sporadic precocious complication appears.

Fig. 2.—Detail of the supra-ambital part of ambulacrum III of a small conical form from the "Lower Chalk."

Fig. 3.—Detail of mid-adoral part of ambulacrum I of a large cylindrical form showing unusual regularity.

Fig. 4.—Plan of ambulacrum II of a specimen from the Upper Greensand (Univ. Coll., Reading, No. 806).

Fig. 5.—Plan of ambulacrum III of a specimen from the *S. varians* zone (Manchester Mus., EARWAKER Collection).

Fig. 6.—Plan of ambulacrum IV of a specimen from the *H. subglobosus* zone (Collection of G. E. DIBLEY, Esq.).

(The three preceding figures are drawn to the same magnification, all the specimens having ambulacra of about the same length. Hence the original of fig. 6 is a younger form than that of fig. 4.)

Fig. 7.—Supra-ambital parts of all five ambulacra of a specimen from the *S. varians* zone (Collection of G. E. DIBLEY, Esq.). Area III is unlike the others in its greater simplicity. A large *Plicatula* obscures part of area II.

## PLATE 67.

Fig. 1.—Plan of ambulacrum V of *Discoidea subuculu*. The apicad plates are rather high, but otherwise the structure is like that of *Plesiechinus*.

Fig. 2.—Plan of ambulacrum I of *D. dixoni* (*R. cuvieri* zone). The magnification is the same as that in fig. 1. The apicad plates are exceedingly high and "Fibulariid," while those of the adoral surface are comparable with those of *Conulus*.

Fig. 3.—Plan of ambulacrum II of a small globular specimen of *Conulus albogalerus* (top of *M. coranguinum* zone).

Fig. 4.—Plan of ambulacrum III of *Micropetalon purpureum* (modified from WESTERGREN, 1911, Plate 29, fig. 6).

Fig. 5.—Plan of ambulacrum II of a young specimen of *Echinonëus cyclostomus* (from WESTERGREN, 1911, Plate 6, fig. 1, *pars*).

Fig. 6.—Plan of ambulacrum II of adult *E. cyclostomus* (from WESTERGREN, 1911, Plate 7, fig. 1, *pars*).

Fig. 7.—Part of ambulacrum of "*Pyrina*" *parryi* (from CLARK and TWITCHELL, 1915, Plate 27, fig. 1F).

Fig. 8.—Adoral part of ambulacrum of very young *Echinonëus* (from WESTERGREN, 1911, Plate 11, fig. 6).

Fig. 9.—Adoral part of ambulacrum of young *Echinonëus* (from WESTERGREN, 1911, Plate 13, fig. 7).

Fig. 10.—Adoral part of ambulacrum of adult *Echinonëus* (from WESTERGREN, 1911, Plate 13, fig. 2).

Fig. 11.—Detail of adapical part of ambulacrum II of *Conulus albogalerus* (Univ. Coll., Reading, No. 803).

Fig. 12.—Detail of adoral part of ambulacrum V of a different specimen of *C. albogalerus*, less highly magnified. The pore-pairs are triserial, and situated in oblique grooves, near the peristome.

## Plate 68.

Fig. 1.—Plan of ambulacrum II of *Galeropygus agariciformis*. The apicad pores are hardly sub-petaloid. There is a hypophyllode adorally.

Fig. 2.—Plan of ambulacrum V of *Nucleolites quadratus*, showing a marked, but restricted, petaloid character adapically, and a complex hypophyllode adorally.

Fig. 3.—Plan of ambulacrum IV of *N. scutatus*, showing a more advanced petaloid character and a simple hypophyllode with apicad demi-plates.

Fig. 4.—Adoral parts of all five areas of *Trematopygus faringdonensis*, showing an extremely diffuse hypophyllode, resulting in structure like that of *Conulus*. The complexity is least in areas I and V (the longest), and greatest (reaching above the ambitus) in area III (the shortest). In column 4, *a* two plate-series show remarkable similarity to the structure of *Discoidea cylindrica*.

Fig. 5.—Detail of mid-adoral parts of ambulacrum II of *Clypeus sinuatus*, showing the "triserial" arrangement of tubercles and pores.

Fig. 6.—Detail of part of the petal of ambulacrum V of *C. sinuatus*, showing the disparity of the pores and simplicity of the plating. (Only the coarser ornament is inserted.)

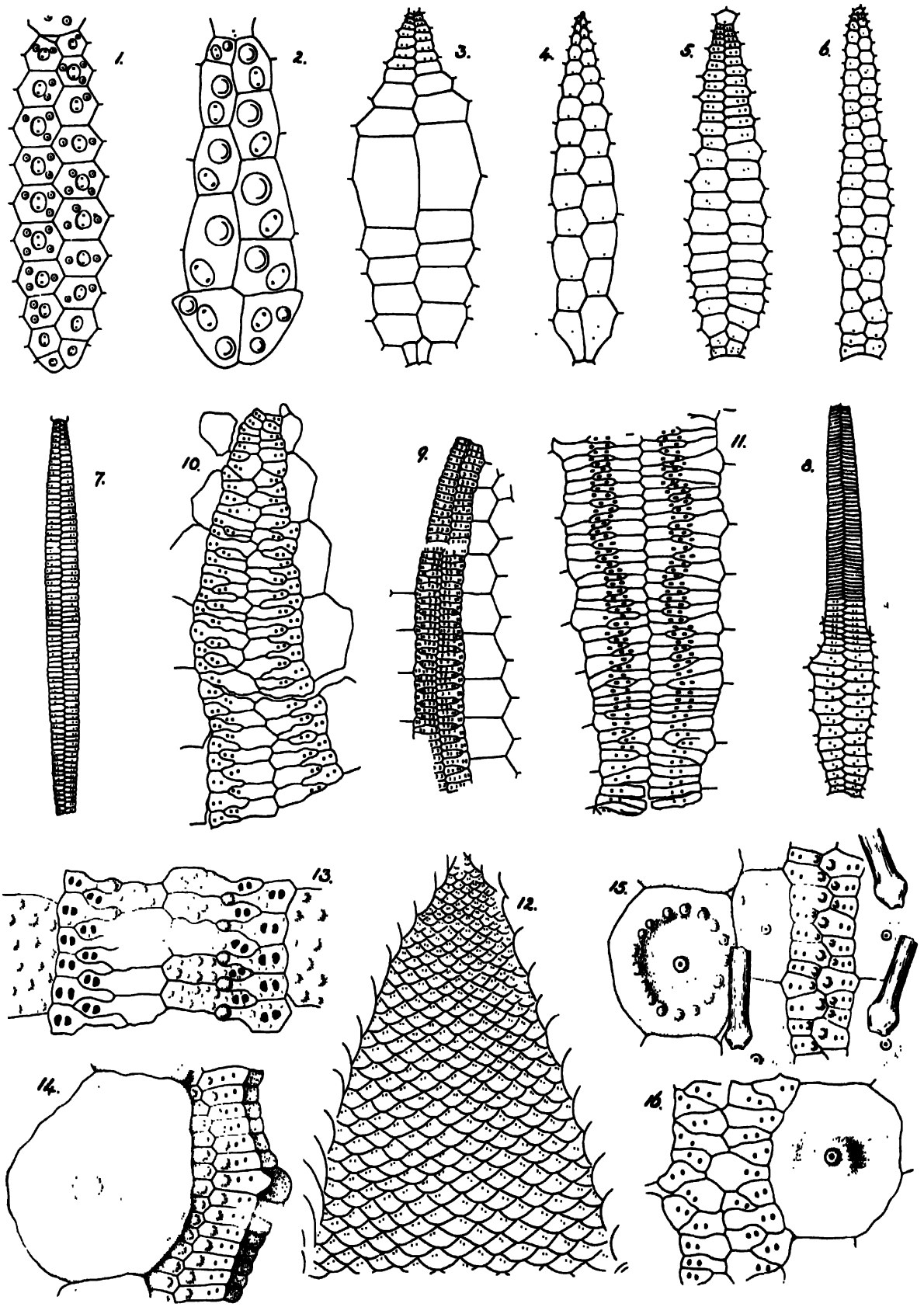
Fig. 7.—Detail of part of the petal of ambulacrum I of *Clypeaster* sp. (Univ. Coll., Reading, No. 638), showing the similarity of the pores and the nature of the demi-plates.

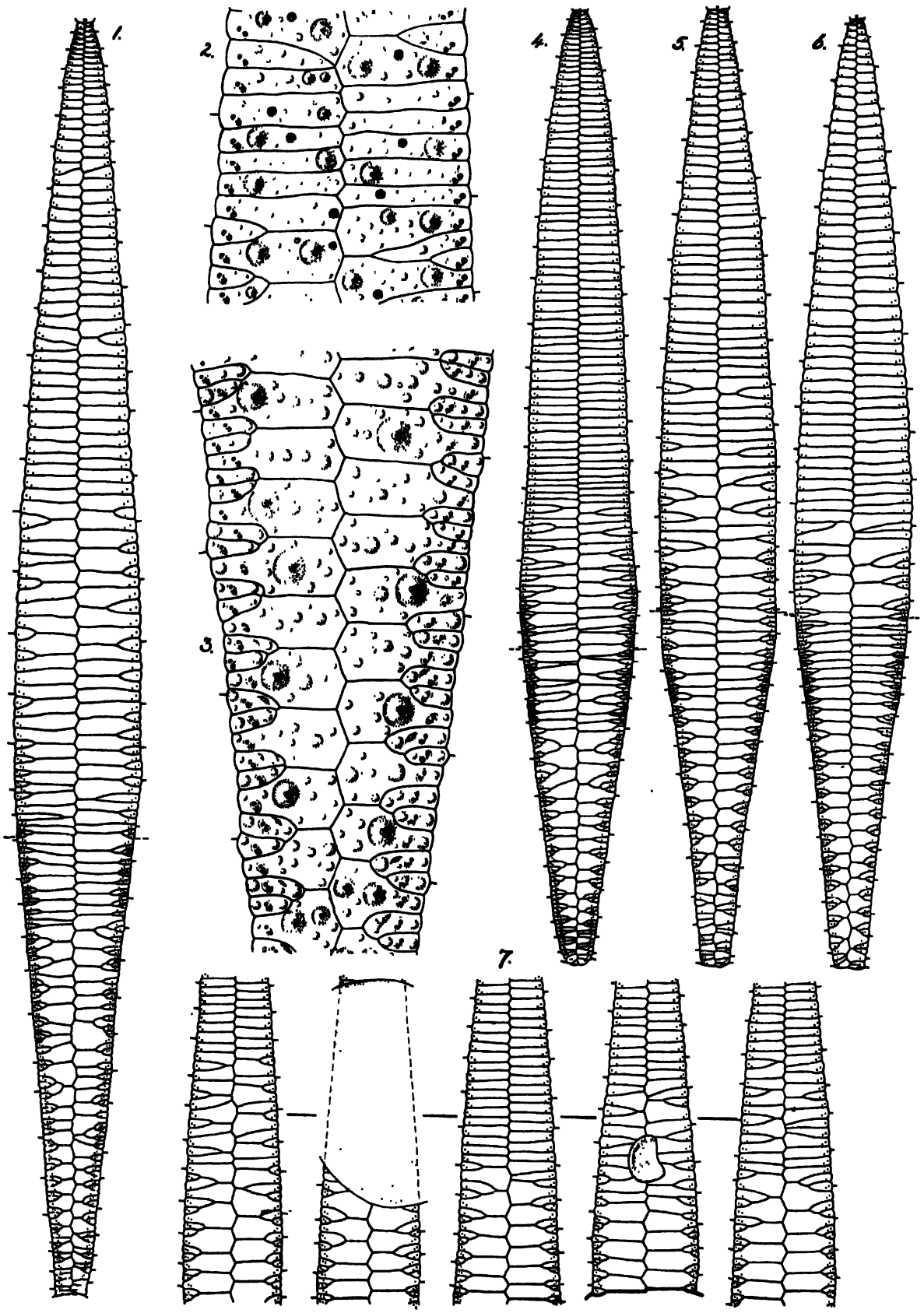
## Plate 69.

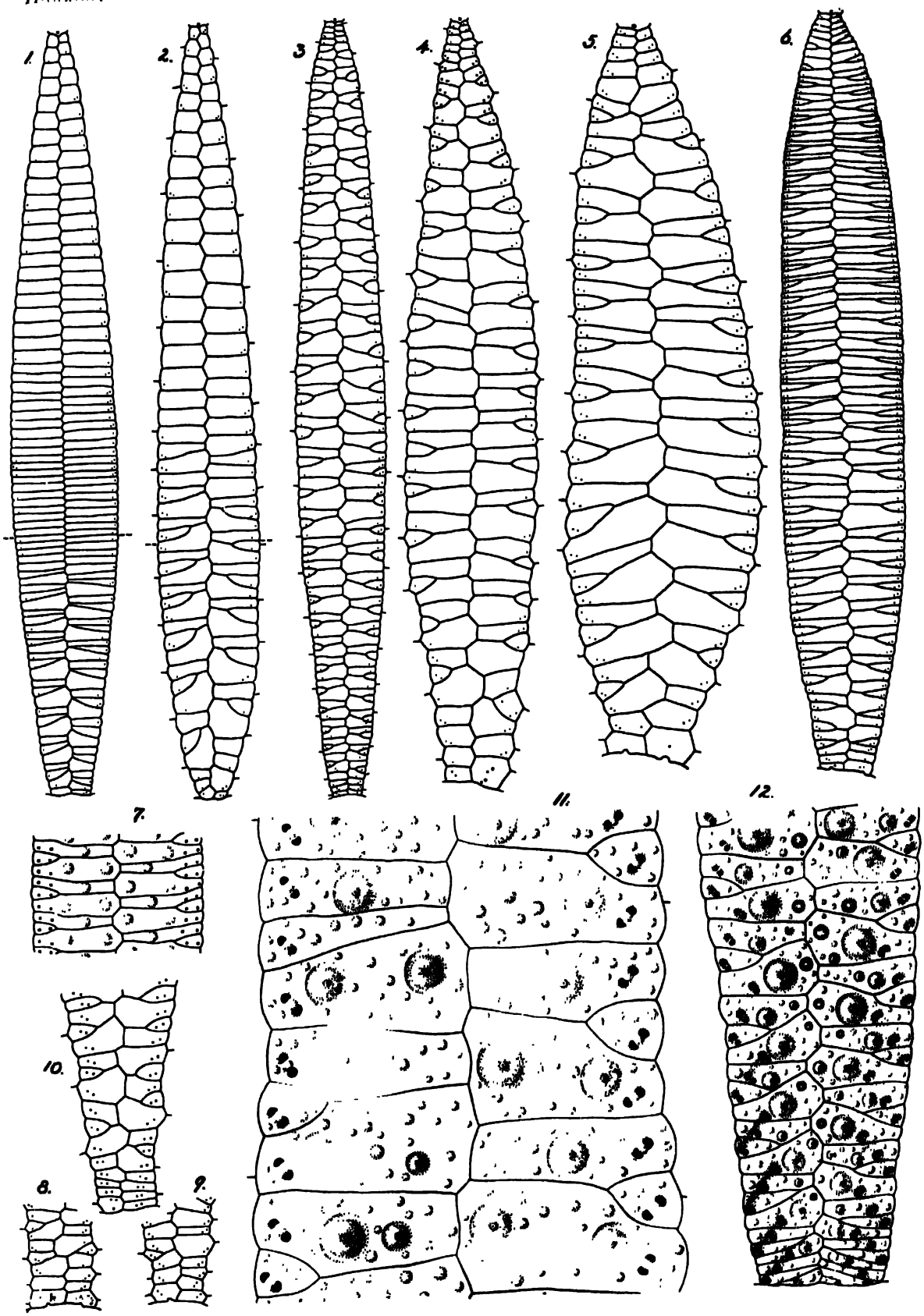
Fig. 1.—Adapical part of the test of an adult *Spatangus purpureus* (drawn from an etched specimen). Ambulacrum III has Bothriocidaroid plating throughout. In some columns of the petals a disturbance in the sequence of the plating occurs, and in one case a demi-plate appears, but in the main the petaloid regions are built of Cidaroid plates.

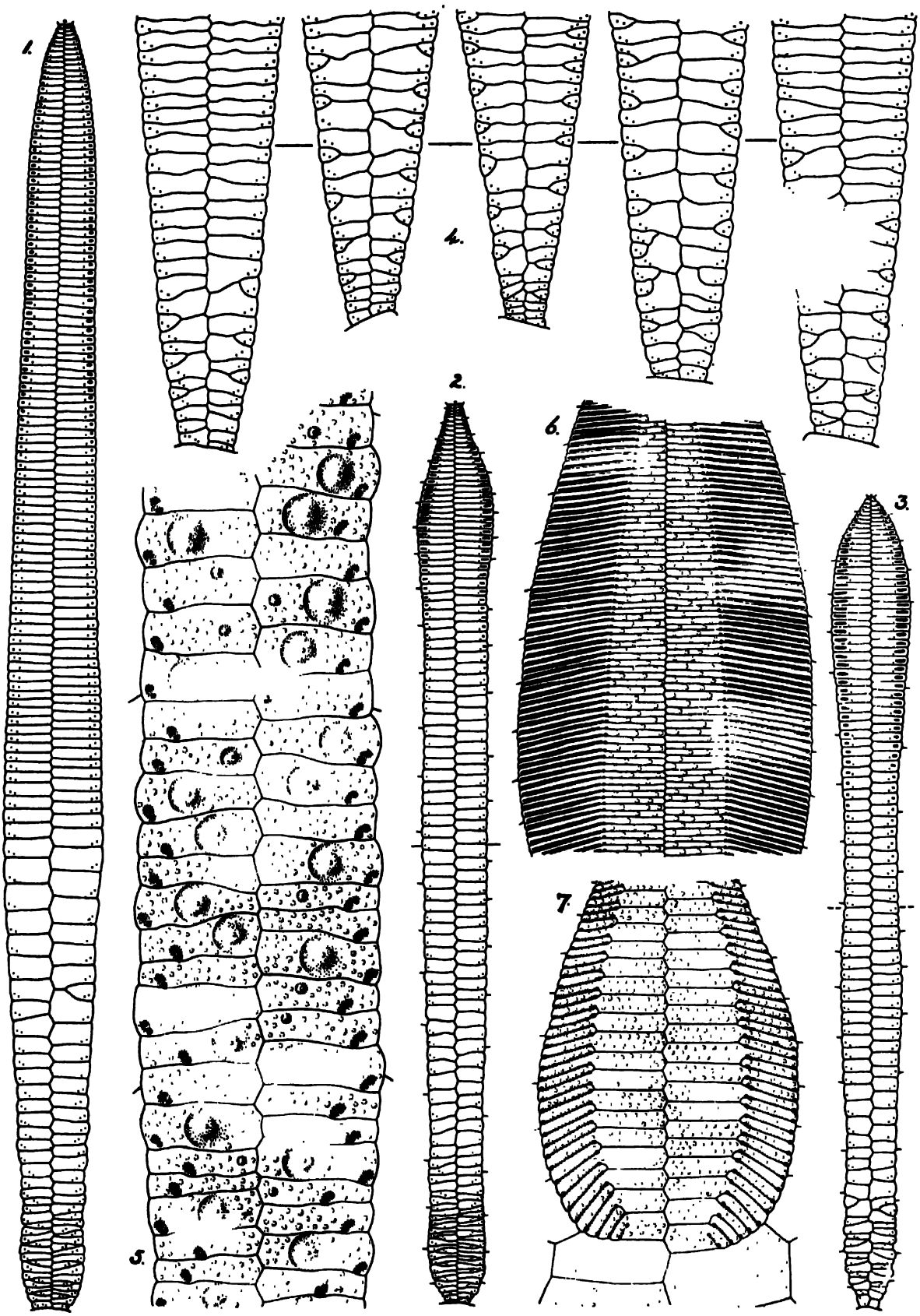
Fig. 2.—Ambulacra III and IV of *Heteraster oblongus* (drawn from a weathered and stained specimen, Univ. Coll., Reading, No. 812). Area III has irregularly arranged alternations of petaloid and non-petaloid pores, the plates bearing the latter being more or less occluded. Area IV has petaloid pores in one column, non-petaloid in the other. The plates of the former are alternately primaries and demi-plates, those of the latter are approximately Bothriocidaroid primaries. There are nearly twice as many plates in the petaloid column as in the other.

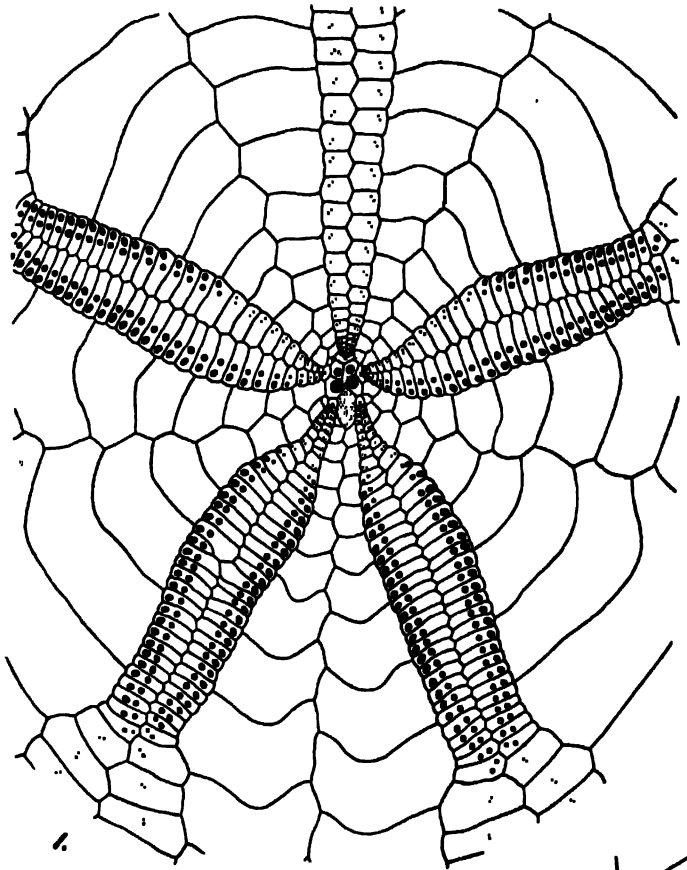
Fig. 3.—Part of ambulacrum (?III) of "*Inaechytes texana*," Cragin (from Clark and Twitchell, 1915, Plate 35, fig. 2, *c*). A similar development to that of area III in fig. 2, but with homogeneous pores.

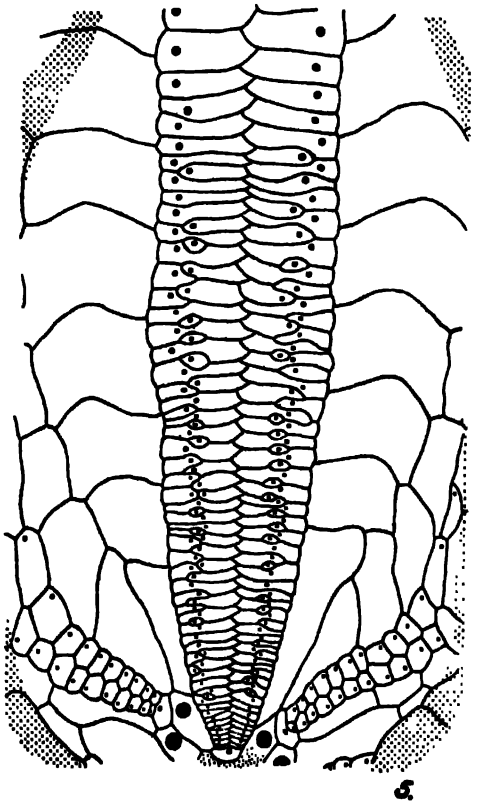

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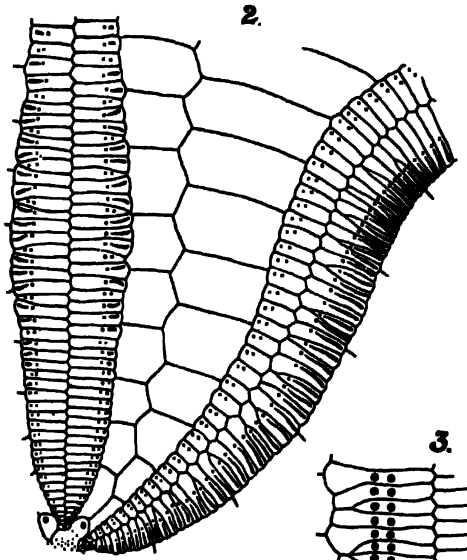

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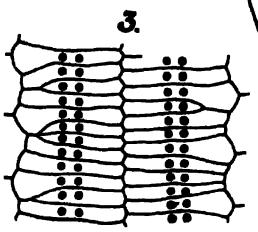

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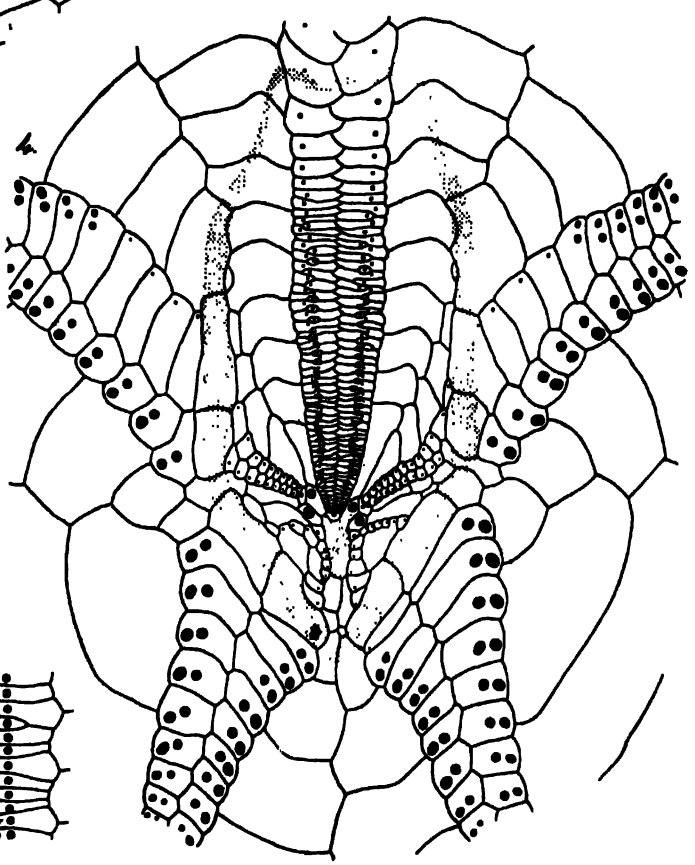

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# XI.—*On the Structure of Lysorophus, as Exposed by Serial Sections.*

*By* W. J. Sollas, *Sc.D., F.R.S., Professor of Geology in the University of Oxford.*

(Received March 17, 1919,—Read May 22, 1919.)

[Plate 70.]

Our knowledge of Lysorophus, the most remarkable land vertebrate, according to Broom, which has been discovered for many years, begins with the description given by Cope,* in 1877, of three isolated vertebræ found in beds of probably Upper Carboniferous age in Vermillion County, Illinois. On the evidence of these vertebræ, Cope regarded Lysorophus as a reptile, and, in 1879,† he doubtfully assigned it to the Clepsydropidæ, a sub-division of the Theromorpha. Case,‡ who had redescribed the vertebræ in 1899, obtained ribs and additional vertebræ from a new locality in the State of Texas, and published an account of them in 1902.§

The same locality afterwards afforded Broili‖ the fragmentary skulls of 14 individuals; and it is to his study of these that we owe our first introduction to the cranial anatomy of the organism. Influenced, unfortunately, by a mistaken interpretation of the occipital region, Broili definitely assigned Lysorophus to the Reptilia, but again misled, this time by the supposed presence of gular plates, which have no existence, he exaggerated the closeness of its alliance with the fishes, and concluded by making it the representative of a new family, which he named the Paterosauria—ancestral reptiles *par excellence*.

Case,¶ having now collected some excellent material from the Texan locality, was able to give an improved account of the structure of the skull, accompanied by excellent figures. With a true instinct, he seized upon the form of the great parasphenoid as stamping it with an indubitable Amphibian character. This contribution evoked a reply from Broili,** who, while modifying his previous

* Cope, E. D., "Description of Extinct Vertebrata from the Permian and Triassic Formations of the United States," 'Proc. Am. Phil. Soc.,' vol. 17, pp. 182–193 (1877).

† Cope, E. D., "Systematic Catalogue of the Species of Vertebrates found in the Beds of the Permian Epoch of North America," 'Trans. Am. Phil. Soc.,' vol. 16, p. 287 (1886).

‡ Case, E. C., "The Vertebrates from the Bone-bed of Vermillion County, Illinois," 'Journ. Geology,' vol. 7, p. 698 (1899).

§ Case, E. C., "Palæontological Notes," 'Journ. Geology,' vol. 10, p. 256 (1902).

‖ Broili, F., "Permische Stegocephalien und Reptilien aus Texas," 'Paläontographica,' vol. 51, pp. 94–97, Taf. XII (1904); "Stammreptilien," 'Anat. Anz.,' vol. 25, p. 579 (1904).

¶ Case, E. C., "Notes on the Skull of *Lysorophus tri-carinatus*, Cope," 'Bulletin Am. Mus. Nat. Hist.,' vol. 24, pp. 531–533, figs. (1908).

** Broili, F., "Systematische und biologische Bemerkungen zu der permischen Gattung Lysorophus," 'Anat. Anz.,' vol. 33, pp. 290–298 (1908).

views, still maintained that Lysorophus was a reptile, and compared it with Amphisbæna.

In the same year appeared a masterly description by WILLISTON.* Based upon a very perfect skull, this is as remarkable for the fulness as for the accuracy of its information. It definitely established the Amphibian nature of Lysorophus, and,

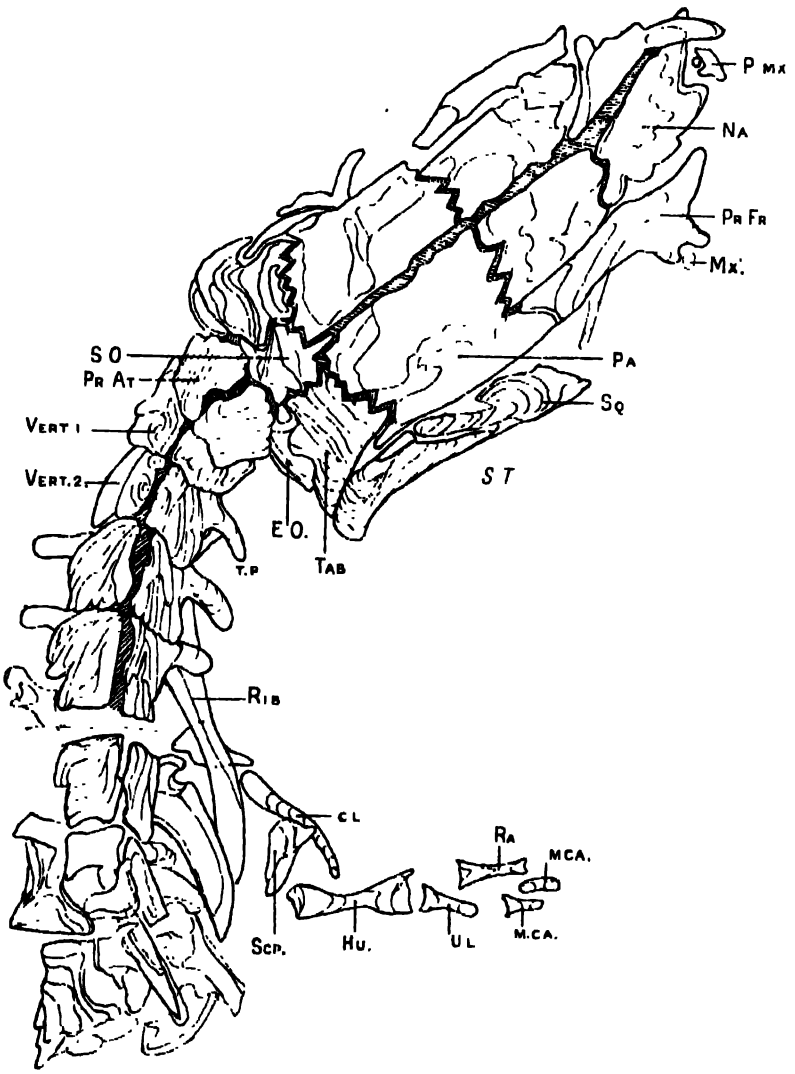



FIG. 1.--Reconstruction of Lysorophus. Dorsal surface. (×5.)

more precisely, even suggested its close alliance with the Urodela; indeed, in a closing paragraph, the author expressed the "conviction . . . that the Lysorophidæ should be included in the Ichthyoidea." A year later, MOODIE,† who has contributed

* WILLISTON, S. W., "Lysorophus, a Permian Urodile," 'Biological Bulletin,' vol. 15, pp. 229–240 (1908).

† MOODIE, ROY L., "Vertebrate Palæontology—The Lysorophidæ," 'The American Naturalist,' vol. 43, pp. 116–119 (1909).

so largely to our knowledge of the Palæozoic Amphibia, expressed his agreement with WILLISTON on the general question, but refused to admit Lysorophus to the Urodela, chiefly on the ground of its long curved ribs, and spoke strongly in favour of its affinity with the Gymnophiona.

In the same paper, MOODIE adds some important information on the age of the

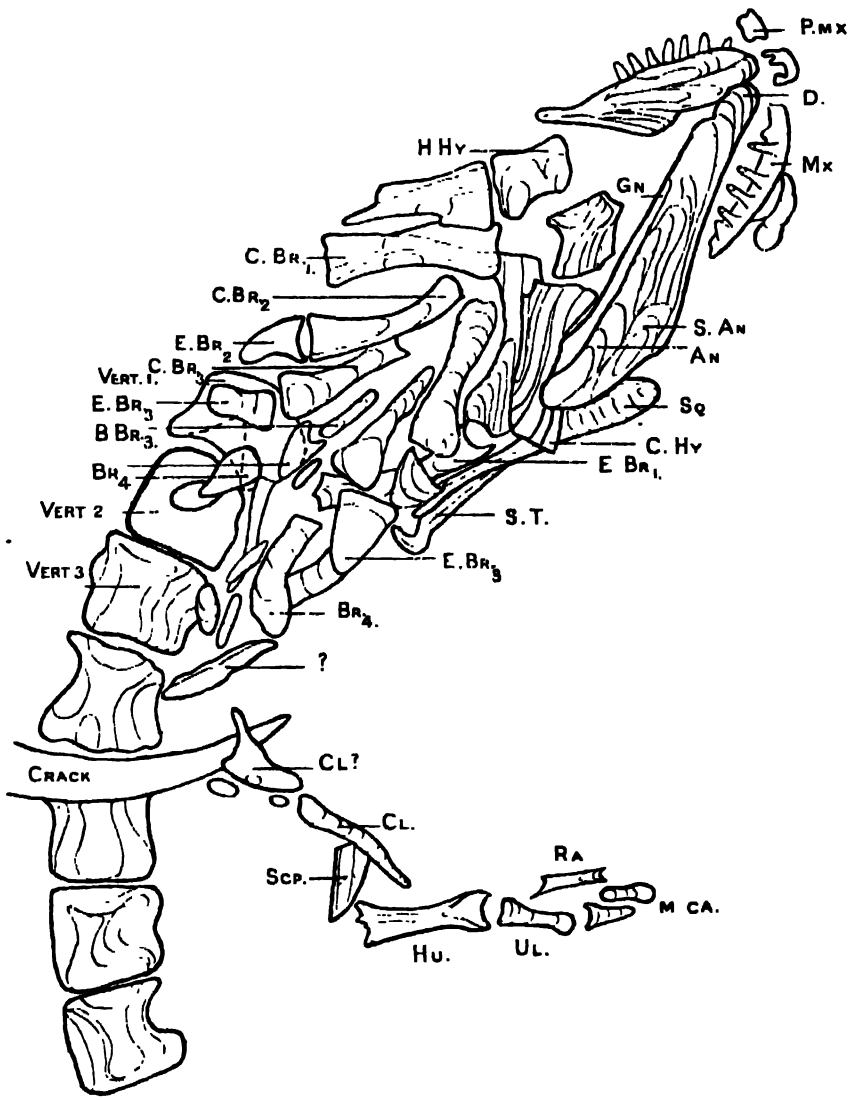



FIG. 2.—Reconstruction of Lysorophus. Vertical surface. (× 5.)

fossil. It appears that the Texan deposits in which Lysorophus occurs are not Permian, as was originally supposed, but Pennsylvanian, probably Upper Pennsylvanian ; thus, Lysorophus would seem to have inhabited North America during Coal Measure times.

Notwithstanding the arguments brought forward by WILLISTON, BROILI*

* KARL A. VON ZITTEL, "Grundzüge der Paläontologie." Neu arbeitet von F. BROILI, E. KOKEN, M. SCHLOSSER. II. Abtheilung, 'Vertebrata,' p. 218. Munich and Berlin, 1911.

evidently remained unconvinced, for, in the edition of ZITTEL'S 'Palæontology,' published in 1911, we find Lysorophus included among the reptiles as a member of the "Paterosauridæ," which is attached to the Squamata. It is illustrated by CASE'S early figures of the skull, with the tabulare interpreted as the squamosal and the anterior cranial walls as the interorbital septum.

In the same year, MOODIE* again expressed his objections to the inclusion of Lysorophus among the Urodeles, alleging that even the presence of limbs, should they be discovered, would not affect his opinion on this important point. He thus met by anticipation the force of the discovery made soon afterwards by Miss MARIAN FINNEY,† to whom we are indebted for a full description of several femurs and other isolated bones of the leg, which were found in association with the now well-known vertebræ.

After a short summary,‡ with an added note retracting a previous statement, WILLISTON returned to the subject in 1912.§ The fact that in this communication Lysorophus is discussed under the heading of "Primitive Reptiles," suggests a change of view, and some conclusions are reached which leave the impression that the author is no longer prepared to maintain his original position intact. Thus, after enumerating its characters, he remarks that, should his account prove to be correct, then "it will necessarily follow that, if Lysorophus is a real reptile, it must occupy a place all by itself as a separate sub-class, without descendants or antecedents." On the other hand, "Lysorophus has no direct ancestral relationships with any modern vertebrates. That the Urodela, or even the Gymnophiona, began in such extremely Amphiuma-like forms in the Carboniferous would be contrary to all . . . experience."

This is far, however, from asserting that Lysophorus is a reptile or that it is not an Amphibian, yet it is easy to understand how a foreigner, like VON HUENE, unacquainted with the niceties of our language, should have interpreted the statement in that sense.

Fortunately, in a later paper, WILLISTON‖ leaves us in no doubt of his views, and definitely places Lysorophus with the Amphibians, as an early offshoot from the Urodele stem.

In 1913, VON HUENE¶ redescribed the skull from specimens in Tübingen and the

* MOODIE, ROY L., "Recent Contributions to a Knowledge of the Extinct Amphibia," 'Am. Nat.,' vol. 45, p. 382 (1911).

† FINNEY, MARIAN, "The Limbs of Lysorophus," 'Journ. Morphology,' vol. 23, pp. 664–667 (1912).

‡ WILLISTON, S. W., "New Permian Reptiles, Rachitomous Vertebræ," 'Journ. Geology,' vol. 18, p. 600 (1910).

§ WILLISTON, S. W., "Primitive Reptiles," 'Journ. Morphology,' vol. 23, p. 640 (1912).

‖ WILLISTON, S. W., "The Phylogeny and Classification of Reptiles," 'Journ. Geology,' vol. 25, p. 411 (1917).

¶ FRIEDRICH VON HUENE, "The Skull Elements of the Permian Tetrapoda in the American Museum of Natural History, New York," 'Bulletin Am. Mus. Nat Hist.,' vol. 32, pp. 315–386, in particular

American Museum ; to new and valuable observations he added some new errors, but recognised, correctly as I believe, its affinity with the Urodeles.

In 1914, my friend, Dr. BROOM, who had seen and appreciated the results already obtained by the employment of serial sections in the elucidation of fossil remains, obtained through the kindness of Dr. MATTHEW, of the American Museum, two specimens of Lysorophus, which he generously presented to me for investigation ; and, still more generously, he placed in my hands at the same time, to dispose of as I might think fit, the MS. of a paper he had himself prepared on the cranial anatomy of this organism. After sections had been prepared of one of the specimens, I found that they confirmed in so striking a manner the most important conclusions in Dr. BROOM's paper that I took immediate steps for its publication.*

Out of much that is new in this communication, we may select for special attention the interpretation of certain deep-seated elements of the skull as ossifications in the cranial cartilage, resembling, at least superficially, the sphenethmoid and alisphenoid or epipterygoid. Dr. BROOM concludes his account with the statement that the skull is "fundamentally Amphibian," with closer alliances to the Urodela than the Anura or Gymnophiona.

Finally, my friend Dr. WATSON, who has made several fresh observations as yet unpublished, informs me that he is convinced from the study of a remarkably well preserved skull in his possession that the Amphibia are the only group to which Lysorophus can be assigned. Dr. WATSON has taken great interest in my work of reconstruction and I am indebted to him for several valuable suggestions. His last visit to Oxford, made when this account was on the verge of completion, had indeed some unexpected consequences, necessitating a change in the nomenclature of the parts associated with the suspensorium. Thus the bone which I, in common with previous investigators, had regarded as the quadrate (fig. 3) was supposed by Dr. WATSON to be completed below on the inner side by a process which is identical with the upper part of a separate bone, identified by me with the articulare of the lower jaw. This led to a re-investigation of the supposed articulare ; it is distinguished by a very narrow "waist" and in one specimen the "waist" has disappeared, so that the upper is no longer continuous with the lower part. Dr. WATSON therefore suggested that the supposed articulare is not a single bone but consists of one bone above the "waist"—the true quadrate, and another below—the true articulare. This was a rather startling interpretation, especially as the identifications already made corresponded very closely with the disposition of the parts as they occur in Amblystoma. It is supported, however, by convincing evidence. Thus, the head of my supposed articulare never articulates with my supposed quadrate but lies between

pp. 322 *et seq.*, and "Ueber Lysorophus aus dem Perm von Texas," 'Anat. Anz.,' vol. 43, pp. 389–396, figs. (1913).

* BROOM, R., "On the Genus Lysorophus, COPE," 'Annals and Magazine of Natural History,' ser. 9, vol. 2, pp. 232–240 (1918). (With a Note by W. J. SOLLAS.)

that bone and the pterygoid, a relation which I had attributed to dislocation. It obtains, however, in all my specimens and in Dr. WATSON'S as well and thus seems too constant to be the result of accident. Further, on a re-examination of sections we found the pterygoid and the false "quadrate" so precisely adapted to the sides of the head of the "articulare" (fig. 20) that such an explanation became impossible and it was necessary to admit that all three bones still retain their original position.

We are thus led to conclude that Dr. WATSON'S view is correct. The bone which had every appearance of being the articulare is in fact two bones, the articulare and the quadrate, which in one of our specimens retain their natural position and articulate with each other.

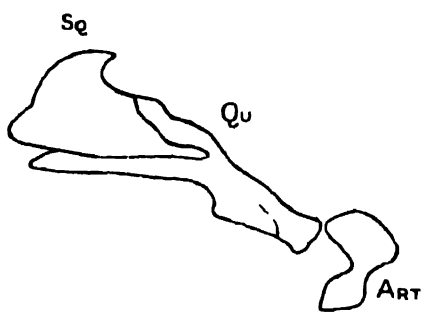



FIG. 3.

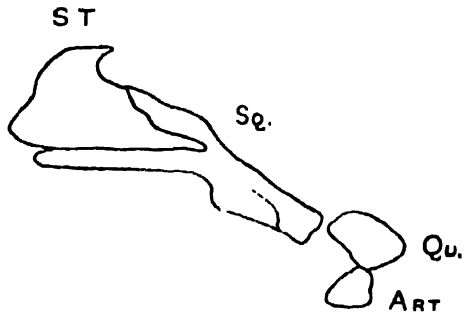



FIG. 4.

FIG. 3.—Original interpretation of the suspensorial region. The "articulare" is displaced towards the right: in its natural position it would be partly concealed by the "quadrate" (×5.)

FIG. 4.—Interpretation now proposed for the suspensorial region. (×5.)

This renders necessary a renewed identification of the bones previously named quadrate and squamosal. Dr. WATSON proposed to call the "quadrate," which bounds the true quadrate on the outer side, quadrato-jugal and for this there may be, no doubt, much to be said. On the other hand the numerous and important features which connect Lysorophus with the Urodeles suggest the squamosal; for in that group it is the squamosal which in all its relations most recalls the bone in question. But if this be admitted then the bone which has hitherto been called "squamosal" becomes the supra-temporal (fig. 4) and in support of this interpretation it may be re-called that PARKER and BETTANY* in their account of the skull of Amblystoma make mention of the fact that on the right side of the specimen which they figure "the postero-superior angle of the squamosal is converted into a distinct small supra-temporal bone."

Lysorophus would thus appear to furnish us with an additional instance of that overlap of the squamosal by the supra-temporal which is so marked a feature in Ichthyosaurus.

Before closing this part of my subject I should like to express my deep sense of the obligations I am under to my friend and colleague, Mr. GOODRICH. In

* PARKER and BETTANY, 'The Morphology of the Skull,' London, p. 126, §301 (1877).

endeavouring to find my way through the difficulties of this investigation I have constantly sought his advice and never in vain. How often he has diverted my steps from deceptive by-paths and concealed pitfalls will be known only to myself.

The specimens presented me by Dr. BROOM had not a very promising appearance: they consisted of two nodules with some of the roofing bones of the skull exposed on the surface. The matrix consisted of a fine red limestone traversed by a network of winding canals. It looked as though the coils of the snake-like creature had been invested with a thick coating of calcareous and ferruginous mud which had subsequently been cemented together by a deposit of calcite.

The nodule which contained the largest head was selected for treatment and in spite of its apparently imperfect consolidation no difficulty was experienced in grinding it down. A complete series of 156 sections were obtained at intervals of 0·1 mm. and these were photographed under an enlargement of 4 diameters. The skull, as well as a series of dorsal vertebræ associated with it, was then reconstructed, first by tracing the sections on glass plates, a very useful preliminary, and afterwards by building it up in plaster.

The results exceeded my expectations and I proceeded to a description of this material with the intention of confining myself to its evidence and so dispensing with the labour of preparing the second specimen. When, however, it appeared necessary to clear up some obscure points, I had to relinquish this intention and obtained a series of 46 sections from the second specimen. These were cut at intervals of 0·2 mm. and photographed under an enlargement of 5 diameters. They exposed the skull, a series of "cervical" and dorsal vertebræ, the right shoulder girdle, and bones of the right fore limb.

These sections proved so much superior to the first, especially by the comparative absence of distortion, that abandoning the figures I had already drawn, I commenced anew and based my description on the reconstruction of the second specimen, using the first merely for confirmation and supplementary information.

Now that we can handle the skull and other parts of the skeleton and examine them on all sides, free from adventitious matter, it is difficult to repress a feeling of æsthetic satisfaction. Every detail of structure is revealed, the several bones are displayed in their original relations as clearly as in a macerated and mounted skeleton, and accidents of fossilization, when they exist, proclaim as a rule their true nature.

There is, I am convinced, a great future for this method, which is bound to add largely to our knowledge of fossils, rendering the study of palæontology more exact and inspiring greater confidence in its results. Many of the mistaken interpretations made by distinguished palæontologists would have been impossible if they had been able to avail themselves of this means.

The drawbacks are more apparent than real. The loss of the original specimen is of little account, for all that can be known of its form and structure is preserved on

photographic plates which can be multiplied at will; thus, like the art of printing, rendering possible a permanent existence which can be ensured by no other means.

The laboriousness of the process has been exaggerated, partly, I fear, by myself, but when owing to the war I had on one occasion to perform all the work of grinding down, photographing, and reconstructing the second specimen without assistance, I was astonished to find that the whole series of operations from start to finish occupied less than three weeks. When it is considered that this single specimen affords all the information that has been accumulated by the repeated study of rich collections by numerous observers, and has even disclosed new and important facts, it becomes clear that the method is not so laborious as it seems. Further, the greater part of the work can be performed by comparatively unskilled labour, and finally the labour expended is recompensed by a certainty which is well worth the pains.

*The Skull.*—The skull may be compared to a wedge-shaped box, broader and deeper behind than in front, and with several apertures in the sides. In specimen No. 1, the length is 20 mm.; the height, 9·5 mm.; and the breadth where broadest, *i.e.*, between the posterior angles formed by the supra-temporal bones, 14 mm.; in specimen No. 2 these numbers become respectively 16 mm., 7 mm., and 9 mm. If the roof be regarded as horizontal then the base rises gently forwards from the basi-occipital bone to the premaxillæ.

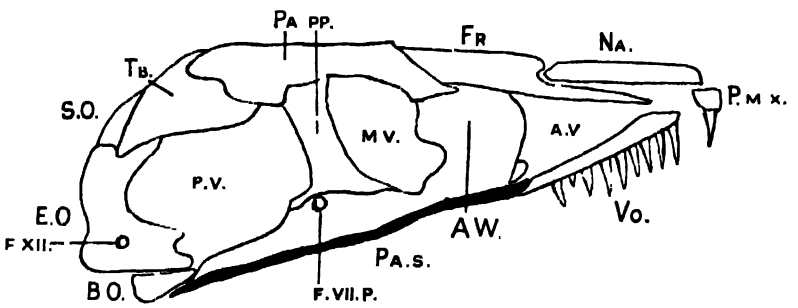



Fig. 5.—Lateral view of the skull with the side bones removed. The symbols which are the same throughout the illustrations are explained on p. 527. (× 5.)

The roof is composed of the nasal, frontal and parietal bones, together with the dorsal part of the supra-occipital and tabulares. It is extended in a kind of eaves over the orbito-temporal region by the prefrontal bone and a lateral process of the parietal.

The floor is formed by the basi-occipital, parasphenoid, and vomers.

The roof is supported from the floor by the following structures taken in order from behind forwards: (i) First by the back of the skull, which is vertical below, where it is constituted by the exoccipital bones, but rounded off above by the forward curvature of the supra-occipital and tabulares. (ii) Next by a pair of pillars (fig. 5, *P.P.*) which rising from a long base on each side of the parasphenoid, and sloping slightly backwards, pass into the parietals. Homologous perhaps with

alisphenoids, these are, in a true sense, "*columellæ cranii*." (iii) Then come a pair of laminæ (fig. 5, *A. W.*), which rise like two walls above the parasphenoid; on the whole bowed slightly outwards, they curl inwards below over the parasphenoid, but remain distinct and separate from it: above they reach the frontals with which they seem to be confluent. They are analogous at least to orbitosphenoids. (iv) Finally, the vomers pass upwards from the ventral face of the anterior extremity of the parasphenoid to end just behind the premaxillæ by which they are linked on to the nasal bones.

Between these supports are three great lateral apertures, the most posterior (fig. 5, *P. V.*) which is the largest lies between the back of the skull and the posterior pillars; save for some minor openings it is completely closed by the pro-otic, opisthotic, stapes, the lateral wing of the tabulare, the supra-temporal, and to a slight extent also by the squamosal (figs. 6, 7).

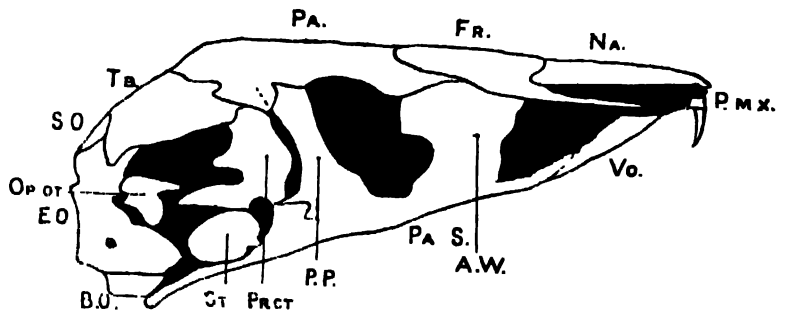



FIG. 6.—Lateral view of the skull showing the ear bones in place. (× 5.)

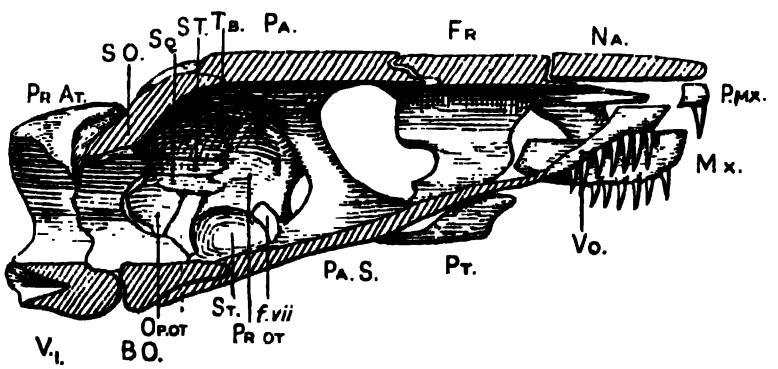



FIG. 7.—The structure of the skull seen from within as exposed by a sagittal section. (× 5.)

The middle aperture (*M. V.*) between the posterior pillars and the anterior walls is vacant. It is of considerable size, and was doubtless occupied during life by cartilage, through which passed the optic and other nerves to the eye.

The anterior aperture (fig. 5, *A. V.*) is very incompletely closed by the ascending wall of the maxilla, and is bridged over by an arch formed by the union of a descending process of the prefrontal and an ascending process of the maxilla.

The occipital segment (fig. 12) presents a large foramen magnum, to the boundary of which the supra-occipital contributes. Above the foramen a small post-temporal fossa occurs on each side, bounded by the supra-occipital, tabulare and exoccipital. The exoccipitals are perforated by a foramen for the twelfth nerve and its associates.

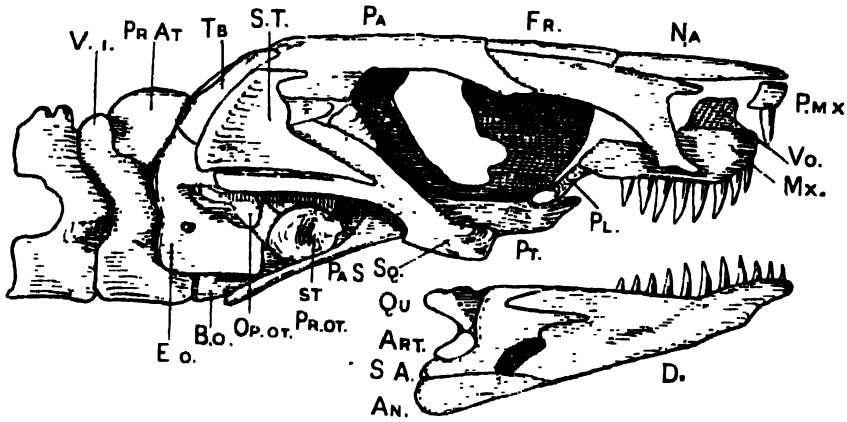



Fig. 8.—Right side of the skull seen from without. (× 5.)

Between the exoccipital and the opisthotic is the jugular foramen, which no doubt gave passage to the tenth nerve.

Between the pro-otic and stapes is an aperture which corresponds to the foramen pro-oticum commune for the fifth and seventh nerves.

The posterior pillars are perforated near the base by a foramen for the palatine branch of the facial nerve.

The space outside the middle aperture was probably the seat of the eye.

The open space of the incompletely closed anterior aperture, in particular that part of it which lies in front of the maxilla, between that bone, the premaxilla, nasal and prefrontal probably included the outer nostril. It is continued downwards and backwards to open between the vomer, maxilla and palatine in a large oval space within which the inner naris was probably situated. That a well-defined external nostril is not expressed in the skeleton is only what we might expect, for in living Urodeles the boundary of this aperture is furnished by the soft parts, and on their disappearance disappears with them.

The curious feature presented by the maxillary prefrontal arch suggests the existence of a tentacular organ, such as occurs in Ichthyophis and is said to be present as a rudiment in Amblystoma,* as well as in the larva of Necturus (Platt). The opening of the space within the arch seems to have been observed by Williston, who suggests that it may have lodged the eye.

The maxilla does not present the free posterior termination so characteristic of the Urodeles, but joins the palatine bone, which is also connected with the posterior end of the vomer and the anterior end of the pterygoid.

* A. Davison, 'Am. Nat.,' vol. 30, p. 648.

Between the posterior third of the pterygoid and the thickened anterior end of the squamosal is lodged the quadrate bone.

The lower jaw consists of the dentary, surangulare, angulare and goniale, all comparatively large bones, and a small articulare.

There is a large hyoid; and the branchial arches, which are at least three in number, more probably four, are well developed, and extend as far back as the middle of the third vertebra.

*Basi-occipital* (figs. 5–9).—This is a comparatively large separate bone, shaped rather like a wedge, broader than long (3·5 mm. by 2 mm.).

Its dorsal surface is horizontal and approximately flat, with a shallow depression at each side for the reception of the heel of the exoccipital.

The ventral surface (fig. 7) shares in the general slope of the base of the skull, *i.e.*, forwards and upwards, and is produced along the middle line into a sharp ridge (measuring 0·8 mm. from base to summit), which is bounded on each side by a wide groove. The ridge projects into and even through the parasphenoid, which fills the channels on each side and completely invests all the rest of the ventral face.

The posterior surface, which is vertical and 1·6 mm. in height, is almost flat, but with a faint though evident depression in the middle, where it is in contact with the "odontoid" of the first vertebra.

The sides of the basi-occipital meet the back in a well marked but rounded angle over the ventral half, but as they continue upwards they flow smoothly into the rounded outline which distinguishes the summit.

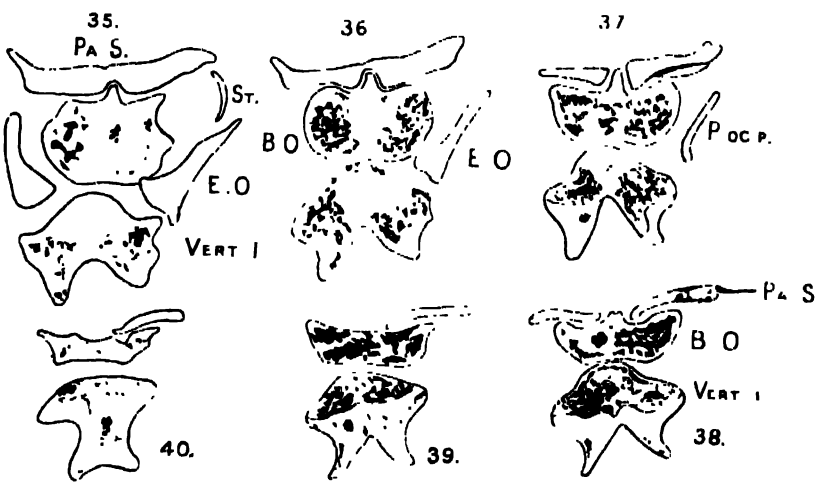



FIG. 9.—A series of horizontal sections through the basi-occipital, the end of the parasphenoid, the first vertebra, the paroccipital process of the exoccipital and the base of the stapes. (× 5.)

*Exoccipital* (figs. 1, 5–8, 10–12).—The exoccipital consists of a short vertical stem which expands above in the plane of the occiput into a plate resembling an inverted triangle—the superior lamina—and below, just before its termination, into a

horizontal plate—the "foot." Its continuation for a short distance further downwards may be termed the "heel."

The stem presents itself in transverse sections as a spherical triangle with one side concave, so that its edges fore and aft are well marked. This concave side forms a large part of the parietes of the foramen magnum which is thus sharply defined before and behind.

The superior lamina is cleft near the summit by the post-temporal fossa into two lateral lobes, one mediad or inner, the other outer.

The inner lobe, which is the narrower, articulates with the supra-occipital, adapting itself on the outside of the skull to an angular incision in the lower margin of this bone, and on the inside to the under surface, which it follows close to the outer edge for a considerable distance forwards.

The outer—or since it articulates with the tabulare—the "tabular" lobe crowns the lamina like a little parapet. It is curved forwards from side to side, thus providing a rounded recess behind to receive the descending termination of the tabulare.

The foot is formed by the expansion of the stem at the front and sides into a horizontal plate; behind there is no noticeable expansion, the back of the stem being continued downwards into the heel.

On each side the foot is produced into a long prong-like process, which is directed forwards. The inner of the two prongs, as well as that part of the plate which lies in front of the stem, is closely applied to the upper surface of the basi-occipital, and the front end of the prong extends beyond the basi-occipital to end against the parasphenoid.

This prong makes the terminal sweep of a well-marked curve, which is continued upwards from it along the front edge of the stem and inner lobe of the exoccipital, and still onwards along the outer margin of the supra-occipital, as exposed on the interior of the skull, up to its termination against the parietal. It probably marks the limit between the brain and the auditory chamber.

The outer prong, a lamelliform process which is applied to the side of the basi-occipital, extends forwards as far as the posterior margin of the fenestra ovalis, to form part of the side of the skull. It also contributes to the support of the opisthotic, and hence may be distinguished as the paroccipital process.

The heel of the exoccipital is applied on its inner side to the posterior upper corner of the basi-occipital, and projecting beyond the back of that bone overlies the interspace between the basi-occipital and the centrum of the first vertebra (fig. 11). It bears a facet which looks downwards and inwards, and articulates with the centrum of the first vertebra, which is excavated at its antero-lateral corner to receive it.

Just above the origin of the foot a slight recess is visible on the inner side of the stem, and at the bottom of this a minute foramen about 0·2 mm. in diameter. This, which is present in all four of the exoccipitals provided by my two specimens,

has been unhesitatingly attributed to the tenth nerve. This interpretation rested, no doubt, on the assumption, now known to be erroneous, that the exoccipital included an opisthotic element. The foramen for the vagus is to be looked for between the exoccipital and the opisthotic, and it is precisely in this position that a large foramen, the jugulare or lacerum posticum, is displayed in our reconstructions. It follows, therefore, that the foramen in the exoccipital itself should be assigned not to the tenth nerve but to the twelfth.

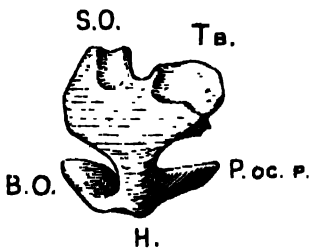



Fig. 10.

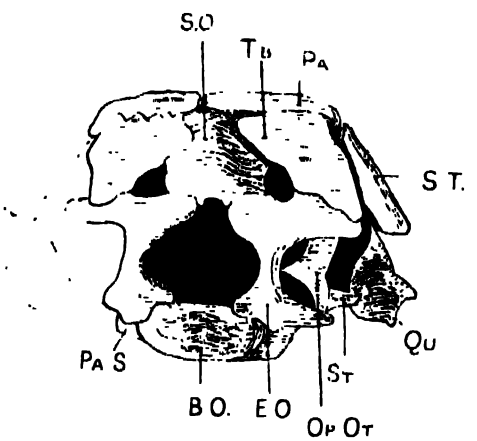



Fig. 12.

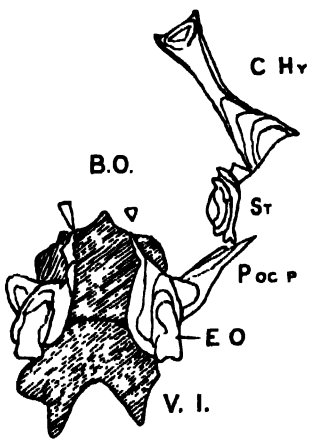



Fig. 11.




Fig. 13.

Fig. 10.—Exoccipital (specimen 1) seen from behind. *H.* the heel; *P.oc. P.* paroccipital process; *B.O.*, *S.O.*, *Tb.* point to the articular facets made by the exoccipital with the bones indicated by these letters. (× 4.)

Fig. 11.—The exoccipitals seated between the basi-occipital and first vertebra. The paroccipital process of the right exoccipital extends as far as the stapes and the stapes is in contact with the ceratohyoid. (× 5.)

Fig. 12.—The back of the skull. (× 5.)

Fig. 13.—The supra-occipital bone. *a*, posterior and superior; *b*, posterior; *c*, anterior surface. (× 5.)

It would seem that the attachment of the exoccipitals to the basi-occipital was not very secure, for in specimen 1 both the exoccipitals are displaced, with a shift to the left, that on the right being at the same time carried forwards, so that its heel now lies over the middle of the basi-occipital. From this specimen alone, it would have been impossible to determine with certainty the true relations of these bones; in specimen 2, however, which is much less distorted, both exoccipitals are in place, and afford harmonious testimony.

*Supra-occipital* (figs. 5–7, 12, 13).—This is a fairly large curved plate, broadest in

the middle, where it measures 4 mm. across. The outer surface, except at the summit, which is flat, is curved from side to side, and rather sharply so in the middle, or, as WILLISTON remarks, it possesses a "median sagittal crest." This crest corresponds with the line along which the two members of the paired pro-atlas meet one another, and its sides are in close apposition with those bones. It is also bounded above by the medial margin of the tabulares.

The inner surface is excavated by a widely open longitudinal channel.

The bone slopes rather rapidly forwards as it ascends, so that its height (2·4 mm.), taken vertically, is less than half its true length (5·5 mm.). Its maximum thickness is about 1 mm.

The lower margin is notched in the middle by the summit of the foramen magnum, and excised on each side for articulation with the exoccipital bones, which extend forwards beneath it.

Above the exoccipitals the margin of the bone bounds the post-temporal fossa, and above this it articulates with the tabulare by a simple serrate suture.

At the summit it articulates with the parietals, also by a serrate suture, one large median tooth being thrust forwards along the sagittal line, while a smaller one on each side enters the parietal bone itself.

The *tabulare* (figs. 1, 5–8, 12, 14) bounds the upper posterior angle of the cranial cavity, and roughly resembles the corner of a shallow box, with the angles inside, filled up and well rounded off.

The "top" articulates in front with the parietal by a serrate suture, and then extends forwards below the suture in a long pointed process, which is received by a groove on the under surface of the parietal.

The "back" curves downwards, overlapping the side of the supra-occipital, with which it articulates, for the first half of its course; it is then notched by the post-temporal vacuity; beyond this it rapidly diminishes in breadth by the retreat of its mediad margin from the middle line, and articulates with the exoccipital, overlapping the tabular lobe of that bone. Its outer margin is comparatively straight, and is bounded by the supra-temporal.

*Parietals.*—The *parietal* (figs. 1, 5–8, 12, 15), which is the largest of the roofing bones, may be described as consisting of a body and its processes. The body, as seen from above, is a roughly rectangular plate, 6·5 mm. long by 4·0 mm. broad in specimen 1, and 5 mm. long by 3·5 mm. broad in specimen 2; in front it articulates by a coarsely serrate suture with the frontal, and by a similar suture with the tabulare behind, as well as with the supra-occipital, which thrusts a long tooth into the sagittal suture. On its outer side the body extends beyond the cranial cavity, roofing over the orbito-temporal region. On its under surface it is thickened immediately in front of the supra-occipital and tabulare, and adapts itself to their margins.

The processes are three in number, one at the antero-lateral angle, one at the postero-lateral angle, and one descending from the middle of the under surface.

The antero-lateral process, which extends forwards, continuing the lateral margin of the body, parallel to the side of the skull, presents two regions: (i) a shorter outer part, which runs forwards and downwards beneath the prefrontal, articulating with that bone by an overlapping suture; and (ii) an inner part, which begins as a forward extension of the body below its serrated union with the frontal—the suture, which is serrate above, thus becoming squamous below—and then continues as a narrow wedge thrust far in between the frontal and prefrontal.

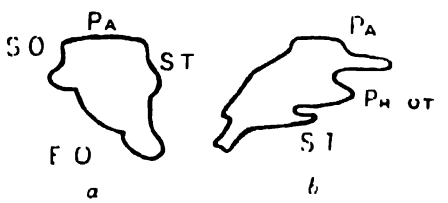



Fig. 14.

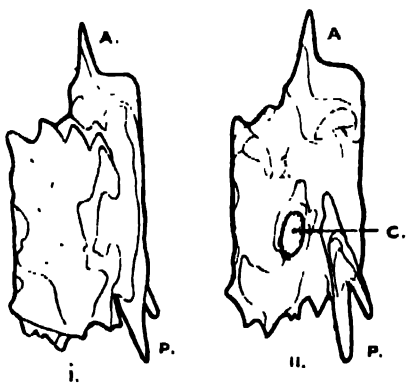



Fig. 15.

Fig. 14.—Right tabulare. *a*, from behind; *b*, from the side. (× 5.)

Fig. 15.—Right parietal bone. i, dorsal; ii, ventral surface. *A*, antero-lateral; *P*, postero-lateral; and *C*, central process. (× 5.)

The posterior process, which extends downwards and backwards, forks into two prongs, one of which is inserted between the tabulare and supra-temporal, while the other adapts itself to the outer edge of the supra-temporal and the summit of the pro-otic.

The central process is continued downwards from the under surface of the body, to form, or contribute to form, a posterior pillar of the skull.

The total length of the parietal, when the processes are included, is 10·5 mm. in specimen 1 and 9 mm. in specimen 2. The thickness of the body is 2 mm. and 1 mm. respectively.

The substance of the bone is traversed by a radiate system of fine canals.

As stated by Williston and others, there is no parietal foramen.

*Frontals* (figs. 1, 5–8, 16).—The frontal as exposed on the surface is also a roughly rectangular bone, 6·3 mm. long, 2·2 mm. broad, and 1·5 mm. thick in specimen 1, and 4 mm. long, 2 mm. broad, 1·2 mm. thick in specimen 2. It articulates with the nasal by a digitate suture above, which extends obliquely downwards and forwards, and is finally replaced by simple overlap. By this anterior extension the length of the bone is increased in specimen 1 to 9 mm.

The outer lateral margin articulates by a simple suture with the prefrontal, and for a short distance with the antero-lateral process of the parietal.

The under surface, near the outer margin, appears to be continued downwards into the anterior wall of the skull.

*Nasals* (figs. 1, 5–8, 17).—In specimen 2 these bones are displaced and not so well preserved as in specimen 1. In the latter they measure 5 mm. in length and 2 mm. in breadth, but only 0·9 mm. in thickness. In front they immediately overlie the premaxillæ, and behind they first overlap the frontals and then articulate with them by a serrate suture (fig. 17).

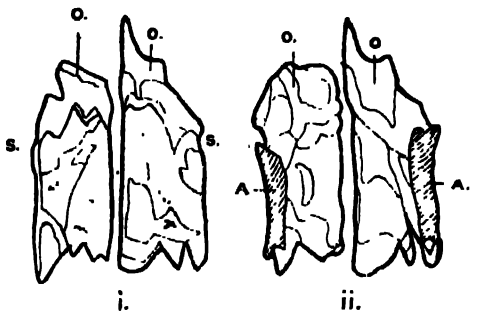



Fig. 16.

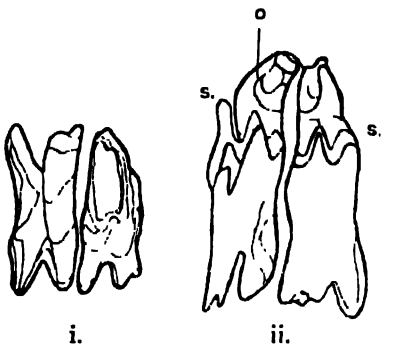



Fig. 17.

Fig. 16.—Frontal bones of specimen 2. i, dorsal; ii, ventral surface. *S.S.*, sutures with nasal bones; *o.o.*, anterior region overlapped by the nasals; *A..A.*, anterior walls of skull. (×5.)

Fig. 17.—i. Nasal and ii, frontal bones of specimen 1, dorsal surface. *S.S.*, serrate sutures of frontal; *o*, region overlapped by nasals. (×4.)

*Prefrontal* (figs. 1, 7, 8, 18).—This bone variously named prefrontal, postfrontal, and lacrimal by investigators of Lysorophus corresponds precisely with that named ectethmoid or lateral ethmoid by Parker in all his work on the Amphibia, but as Parker has identified the ectethmoid with the prefrontal of the higher Tetrapods, we may adopt the latter term as most in accordance with established usage.

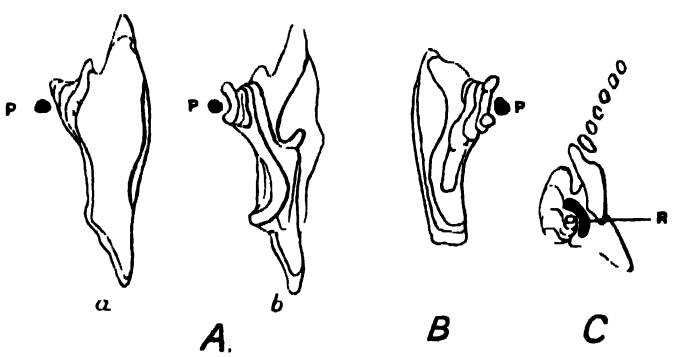



Fig. 18.—A. Left prefrontal bone of specimen 1. *a*, seen from above; *b*, from below (reversed); *p*, articulating process of the maxilla. (×4.) B. Right prefrontal of specimen 2, seen from below (reversed). (×5.) C. Left maxilla of specimen 1; *r*, articular process of prefrontal. (×4.)

The prefrontal (figs. 1, 8, 18), forms a considerable part of the roof or eaves of the skull; articulating behind by overlap with the anterior lateral process of the parietal, it extends forwards along the whole of the outer margin of the frontal, with which it articulates by a simple straight suture, and then continuing still

further flanks the nasal for more than half its length. The anterior rather pointed termination of the prefrontal lies over the suture of the premaxilla with the maxilla.

The under surface (fig. 18, *b*), is excavated by a long shallow sinus and thickened by a longitudinal curved ridge, the anterior end of which is produced downwards into a strong process. This curves outwards as it descends, diminishes in breadth, and is grooved on its outer face for the reception of the attenuated rod-like end of a process which arises from the maxilla to meet it. In specimen 1 the suture so effected extends through 11 sections, *i.e.*, for 1·1 mm., or about three-quarters of the total height of the C-shaped bar formed by the united processes.

*Parasphenoid* (figs. 5–8, 12, 19, 20).—The general form of this bone is shown in fig. 19. In specimen 1 it measures 13 mm., and in specimen 2 11 mm. in length. Its broadest part lies between the basi-occipital and the cranial pillars* (6·2 mm. in specimen 1 and 5·6 mm. in specimen 2); beyond the pillars it becomes rapidly narrower and then maintains a fairly uniform breadth (4 mm. in specimen 1, 3 mm. in specimen 2) till it diminishes to a pointed extremity. The broader part is dentate or notched as in some modern Urodeles, giving it an appearance which in those forms is described by PARKER as "foliaceous."

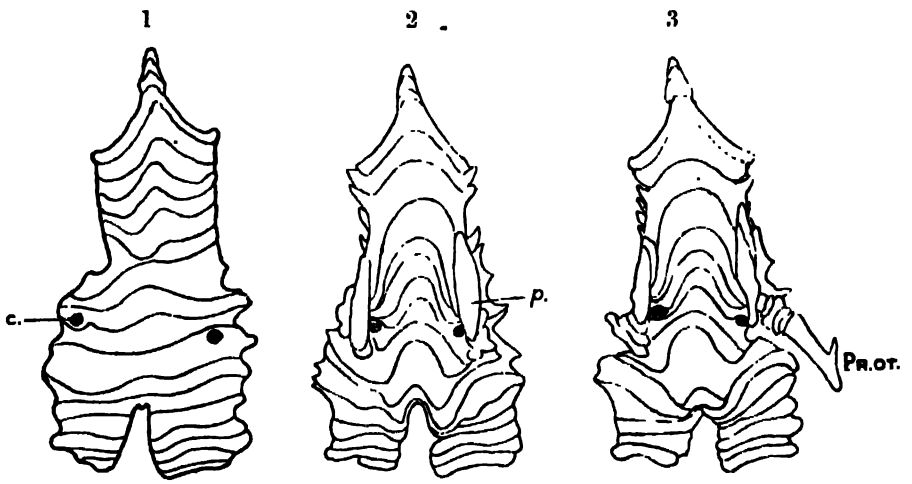



FIG. 19.—The Parasphenoid. i, ventral; ii, dorsal surface; iii, dorsal surface with the basal process of the pro-otic; *c.c.*, foramina for carotid artery; *p.*, base of posterior pillars. (×5.)

The broader moiety of the ventral surface is fairly flat, but as it passes into the narrower moiety it rises into a median longitudinal ridge, bounded on each side by a gentle depression; as these features are continued forward they become slightly more accentuated.

Posteriorly the parasphenoid overlaps the whole of the ventral surface of the basi-occipital except the central ridge and the region immediately behind this. It is thus divided here into two lobes the outer margins of which extend beyond the sides of the invested bone.

* See fig. 20, p. 499.

The dorsal surface is also fairly flat over the posterior moiety, but as it passes forwards between the pillars it takes the form of a shallow median trough as shown in the transverse section (fig. 24) obtained from specimen 1.

The trough is continued forward without much change till it flattens out in front; the anterior walls which are based upon its sides may be clearly distinguished from it. Traced backwards from here its sides gradually rise to pass into the posterior pillars. My sections show no trace of a suture, but on pointing this out to Dr. Watson he made a close examination of a very perfect specimen of his own, which he has developed by skilful chiselling, and succeeded in discovering one. By his kindness I am able to represent this in fig. 23.

Two openings (0·3 mm. in diameter) are visible on the ventral surface, just in front of its greatest breadth, one on each side and not far from the margin. Their course as they traverse the bone is slightly forwards and a little inwards and they reach the dorsal surface close to the sides of the median trough. These are evidently the foramina for the internal carotid arteries.

In Amia and the Frog they occupy much the same position but lie outside the parasphenoid, just in front of the "guard" of that dagger-shaped bone.

Nothing that could be construed as a basisphenoid or a presphenoid or a depression for the pituitary body exists above the parasphenoid.

*The Anterior Walls* (figs. 5–8, 20, 21).—On each side of the skull a bony wall rises from above the anterior third of the parasphenoid and extends to the frontal above.

At its base each wall is 3 mm. in length, about a third of the way up it is reduced to 2 mm. by a notch in the posterior margin and then increases to 4 mm. before passing into the frontal. It is from 2·4 to 2·8 mm. in height and 0·75 mm. in thickness. The posterior notch was probably occupied in the living animal by the cartilage which completed the cranial wall and was perforated in this region by the optic nerve.

The outer side of the wall is a nearly plane surface, leaning only a little out of the perpendicular or bowed outwards as it ascends. The inner side is curved and with the frontals and its fellow wall bounds a tubular cavity narrow at the base and much wider at the summit.

The foot of each wall is produced in front and on the inner side into a horizontal plate which curves inwards and downwards towards the middle line till the two feet nearly meet. In specimen 1 they extend beyond it, overlapping each other, but this is clearly due to displacement.

The shallow cavity of the parasphenoidal trough, originally no doubt occupied by cartilage, is roofed over by these plates, which were evidently not directly connected with the parasphenoid bone.

The relation of the wall to the frontal is less clear; the existence of a suture can neither be asserted nor denied, but in any case the two bones are closely connected.

The walls certainly occupy the region of the sphenethmoid or orbitosphenoid, but it would be rash to identify them with either of these two bones, especially as WIEDERSHEIM* has described similar structures in *Amphiuma tridactylum* as mere downward processes of the frontal, and the figure which he gives in illustration (fig. 22)

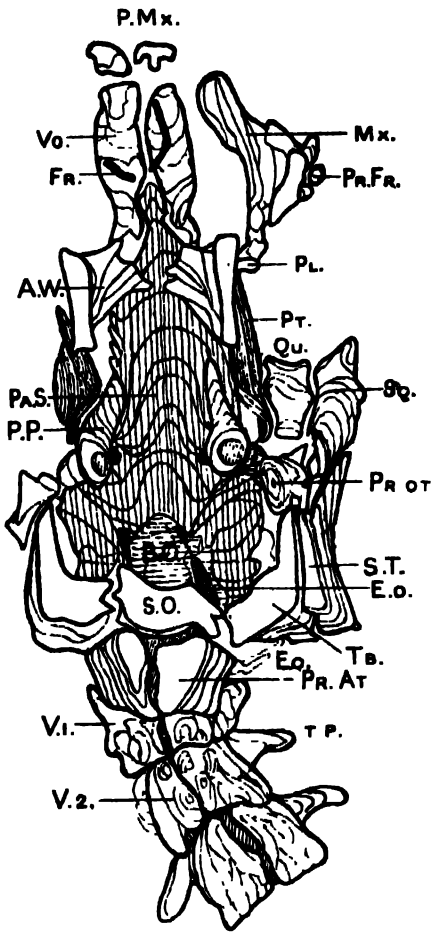



FIG. 20.

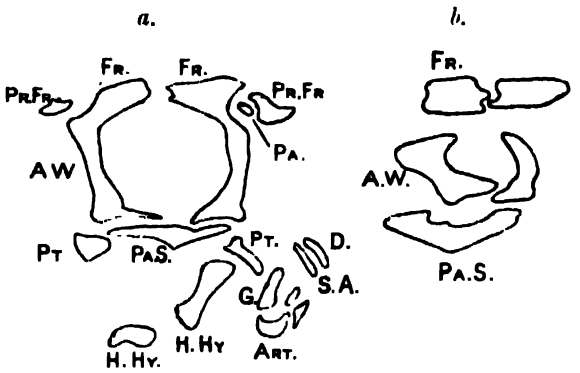



FIG. 21.

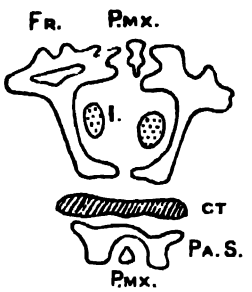



FIG. 22.

FIG. 20.—The skull seen from above with the roofing bones removed. (× 5.)

FIG. 21.—Transverse section of the skull. *a*, of specimen 2 through the anterior walls. (× 5.) *b*, of specimen 1. (× 4.)

FIG. 22.—Transverse section of the skull of Amphiuma after WIEDERSHEIM. I, olfactory nerves; *CT.*, cartilage.

might almost serve for Lysorophus. In Amphiuma, however, the walls as they continue forward shift their origin from the middle of the frontal to its inner edge and thus becoming approximated give rise to an inter-nasal septum. Nothing corresponding to this exists in Lysorophus.

* WIEDERSHEIM, R., "Das Kopfskelet der Urodelen," 'Morphologisches Jahrbuch,' vol. 3, p. 403, Plate XXII, fig. 60 (1877).

We know very little about the embryological development of the processes in Amphiuma. HAY,* who has studied some early stages of Amphiuma, describes the frontals in larvæ (45 mm. in length) extracted from the egg capsule as mere splints; but in a young specimen (6 inches in length) the processes were found to be already well developed and in continuity with the frontals. So far as it goes this would indicate that the processes are of the nature ascribed to them and not independent elements. As the skull of this young specimen was already, however, almost as well ossified as in the adult the evidence is not conclusive and we must await the investigation of intermediate stages to determine this question.

It may be remarked that the absence of any coalescence of the walls with the parasphenoid is a character that the frontal processes share with the sphenethnoid of the Urodeles but not of the Anura.

A good figure of the anterior walls, as seen from the side, has been given by CASE† who mistook them, however, for an inter-orbital septum. BROOM‡ first suggested that they are ossifications in the cartilaginous brain case.

(*Postscript.*—After a re-examination of sections, I find that the anterior walls are not confluent with the frontal bones in specimen 1, but are separated from them by a considerable interval (fig. 21). It is almost certain therefore that their union with the frontals was by suture, and we may now fairly regard them as orbito-sphenoids.)

*The Posterior Pillars* (figs. 5–8, 20, 23, 24).—Each of these columnar bones presents a more or less cylindrical form at the summit, but as it descends it is

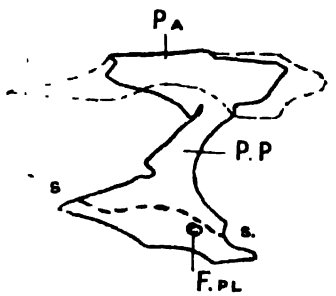



FIG. 23.

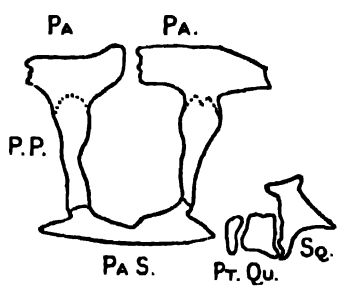



FIG. 24.

FIG. 23.—Longitudinal section through a posterior pillar. (× 5.) *S.S.*, suture observed by Dr. WATSON; *F. pl.*, foramen for palatine nerve.

FIG. 24.—Transverse section through the skull in the region of the posterior pillars. Specimen 1. (× 4.)

sharpened in front, while remaining round behind; on the inner face, in front, it is excavated by a well-marked groove, which continues downwards till the pillar, greatly compressed from side to side, passes into the wall-like region of the base.

* HAY, O. P., "The Skeletal Anatomy of Amphiuma during its Earlier Stages," 'Journ. Morphology,' vol. 4, pp. 10–34 (1891).

† CASE, E. C., 1908, *op. cit.*

‡ BROOM, R., *op. cit.*, p. 235.

Here, immediately above the entrance of the carotid canal into the cranial cavity and close to the anterior spur of the pro-otic is a rather deep recess, opening by a short canal (0·4 mm. in diameter), which runs obliquely forwards and outwards to the exterior, and is then continued as a groove along the outer margin of the parasphenoid. This must be the foramen for the palatine branch of the facial nerve, and the recess probably lodged the anterior end of the ganglion pro-oticum commune.

The pillar appears at first sight to be a simple extension downwards of the median parietal process, but an examination of sections strongly suggests the presence of a suture. For at the upper end sections transverse to the pillar reveal an outer layer of bone, which continues the wall of the pillar upwards, and surrounds an inner style which, increasing in diameter as it ascends, passes finally into the parietal. Between this style and its ensheathing wall is a vacant interval.

The union of the base of the pillar with the parasphenoid is accomplished, as Dr. WATSON has shown, by suture.

The homology of this bone is by no means clear. I have already* named it provisionally "alisphenoid," yet it certainly resembles very closely the epipterygoid of the Chelonia, both in form and its relation to the parietal. Here, however, attention may be called to the view† which would identify the epipterygoid of the reptiles with the alisphenoid of the mammals. In all three cases, Lysorophus, the mammals, and reptiles, we are concerned with a bone having similar relations with the parietal, and so far as we know with the cranial nerves. Differences arise when we pass to the base: in the mammals it articulates below with the basi-sphenoid and pterygoid, in reptiles with the pterygoid, and in Lysorophus with the parasphenoid. In this character by which the pillar of Lysorophus differs from the analogous bones of mammals and reptiles it agrees with the "alisphenoid" of the bony fishes.

On the other hand, in the bony fishes, when it articulates above, it does so not with the parietal but the frontal bone.

It is tempting to suppose that throughout the Tetrapoda we have before us the same bone, whether it is called columella or alisphenoid; that it has persisted in position between the branches of the fifth nerve owing to the important function it has to fulfil in that region as a support, and consequently that it has had to find attachment where it could. In Lysorophus where there is no basisphenoid, and the pterygoid is but feebly developed, the parasphenoid is its only resource; in the

* BROOM, R., *op. cit.* Note by W. J. SOLLAS.

† BROOM, R., 'Proc. Linn. Soc., N.S.W.,' vol. 34, p. 211 (1909); *ibid.*, "The Homology of the Mammalian Alisphenoid bone," 'Rep. S. African Assn. for the Advancement of Science,' 1907, pp. 114–115 (1908); "On the Structure of the Skull in the Cynodont Reptiles," 'Proc. Zool. Soc.,' p. 922 (1911), and in Appendix to W. K. GREGORY, "Report of the Committee on the Nomenclature of the Cranial Bones in the Permian Tetrapoda," 'Bull. Geol. Soc. Am.,' vol. 28, p. 977 (1917); W. K. GREGORY, "Critique of Recent Work on the Morphology of the Vertebrate Skull," 'Journ. Morphology,' vol. 19, p. 1 (1913).

Chelonia, where the basisphenoid is very narrow in front, it falls back upon the encroaching pterygoid.

On the other hand the embryological investigations of Dr. WATSON* have furnished weighty evidence which is opposed to the suggested identification, and as regards the posterior pillar of Lysorophus in particular, he informs me that according to observations of his own, not yet published, a cartilaginous rod is present in the original walls of the vertebrate skull, which makes its last appearance as the Tænia clina-orbitalis of the Monotremes, and is extremely persistent in some reptiles as well as in Cœcilia and probably some fishes. It is as an ossification of this rod that he regards the posterior pillar.

*Pro-otic* (figs. 6–8, 20, 25, 26).—The upper moiety of this rather complicated bone is a stout pillar which articulates above with the under surface of the posterior descending process of the parietal, and touches the anterior edge of the lateral wall of the tabular behind.

In transverse section the pillar presents in this region a rather rounded outline,

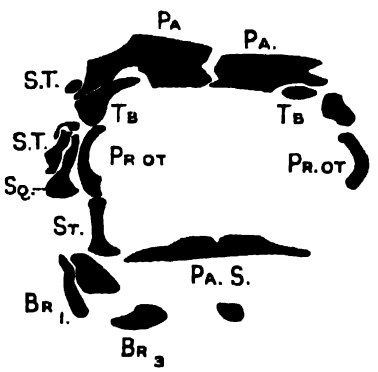



FIG. 25.—Transverse section of the skull passing through the pro-otic and the stapes. (× 5.)

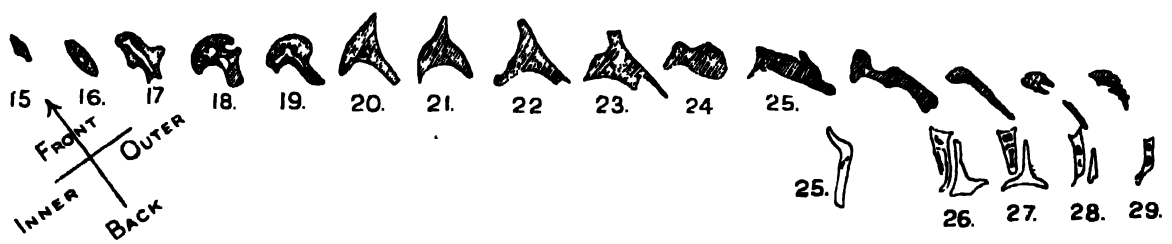



FIG. 26.—The right pro-otic and opisthotic bones in a series of transverse sections taken in order from above downwards. The pro-otic, in the upper line, is distinguished by hatching. (× 5)

but as it descends it is almost immediately produced, at first posteriorly and then anteriorly as well into an alar expansion, and thus acquires a triradiate form; in other words, it becomes a triangular prism with two of its edges produced into long

* WATSON, D. M. S., in "Second Report of the Committee on the Nomenclature of the Cranial Elements in the Permian Tetrapoda," 'Bull. Geol. Soc. Am.,' vol. 28, p. 980 (1916); *ibid.*, "On the Monotreme Skull, a Contribution to Mammalian Morphogenesis," 'Phil. Trans.,' Ser. B, vol. 207, pp. 311–374 (1916).

flanges. The anterior and the posterior flanges lie nearly in the same plane and form the outer side of the pillar which is closely applied to the inner surface of the squamosal.

The face between the inner edge and the posterior flange is hollowed out into a wide groove looking backwards into the interior of the skull. This extends down the greater part of the length of the column, expanding below into the general concavity of the base.

The inner edge or ridge enlarges at its base into a short slender bar which runs forwards and inwards to unite with the posterior pillar, just above its base and the foramen for the palatine nerve. This is not the "alisphenoidal spur of the pro-otic" of PARKER and BETTANY,* for that process extends forwards along the upper edge of the cranial wall while this is directed towards its base. It is notched underneath, just in front of the stapes, for the passage of the seventh nerve, and immediately below its origin the bone is continued backwards as a curved lamella which extends as far as the opisthotic, and contributes to the boundary of the auditory capsule.

The *Stapes* (figs. 6–8, 11, 12, 25, 28).—This elegant little bone resembles a shallow bowl, with a straight handle projecting from the edge. The opercular bowl lies immediately below the posterior lamina of the pro-otic, as though forming its continuation. The handle—"processus opercularis"—is produced from the summit of the anterior edge, and points outwards perpendicular to the wall of the skull. Thus the resemblance of the bone both in form and position to the stapes of a Urodele is complete. In specimen 1 the stapes is displaced, and lies isolated at some distance from the pro-otic. It is traversed by 20 sections (68 to 88), and the vertical diameter is therefore 2 mm. in length; the horizontal diameter measures 2·5 mm. In specimen 2 these quantities become 2 mm. and 1·4 mm. respectively.

The *opisthotic* (figs. 6–8, 26, 27).—Immediately behind the pro-otic is a small




FIG. 27.

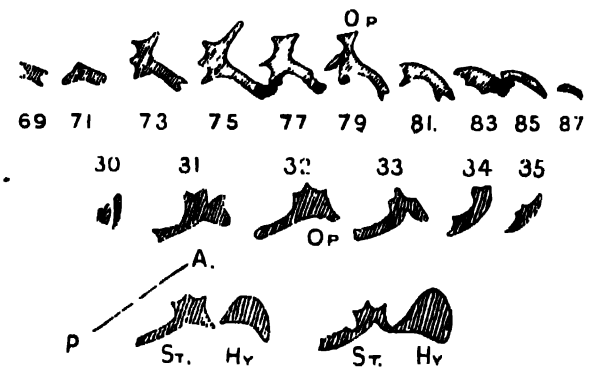



FIG. 28.

FIG. 27.—*a*, Pro-otic and *b*, opisthotic bone, canal through opisthotic indicated by dotted lines. (×5.)

FIG. 28.—Horizontal sections of the Stapes in order from above downwards. 69 to 87. From specimen 1. (×4.) 30 to 35. From specimen 2. (×5.) The sections in the third line show the relation of the Stapes to the Cerato-hyal. *O.P.*, opercular process; *P.—A.*, direction of axis of skull; *P*, posterior; *A*, anterior.

* PARKER and BETTANY, 'Morphology of the Skull,' London, 1877, p. 115, §280.

triangular lamina of bone, curved from side to side, and contributing, together with the pro-otic lamina, to the almost semicircular boundary of the auditory recess.

It is supported below by the outer prong, or paroccipital process of the exoccipital foot, and affixed above to the under edge of the tabular lobe of the exoccipital. It thus fills the larger part of the lateral vacuity which lies between these two occipital processes, leaving, however, an open space between its posterior margin and the exoccipital stem. This is nearly divided into two, an upper and a lower portion, by a spur of the opisthotic; it is this lower portion which we identify with the jugular foramen.

It is scarcely necessary to comment on the interest attaching to this additional example of a separate opisthotic bone, common enough, no doubt, among the primitive reptiles of Permian and Carboniferous times– WILLISTON* regards it as one of their constant characters—but subsequently never met wth, except in the Chelonia and Ichthyosauria.

*Squamosal* (figs. 1, 3, 4, 7, 8, 12, 24, 25, 29).—In this we may distinguish an anterior pedicel from a posterior lamella.

The lamella expands upwards as it proceeds backwards, and is excavated behind by a deep notch with jagged margins. It is firmly wedged in between the pro-otic on the one hand and the supra-temporal on the other.

The pedicel, which in the upper part of its course may be regarded as the thickened edge of the lamella, runs downwards and forwards, and, on passing beyond the lamella, increases in thickness, gives off an alar process from its posterior inner edge, and terminates in a bevelled surface.

The posterior surface of the pedicel is hollowed out by a longitudinal groove, bounded on the inner side by the alar process. Behind this groove, and close to it, rises the ascending ramus of the cerato-hyal. In Necturus and other Urodeles, the epi-hyal end of the cartilaginous hyoid is similarly related to the suspensorium, and the squamosal, which in this form descends as far as the articulation of the lower jaw, is grooved for its attachment.

The squamosal of Lysorophus recalls that of Proteus, as described by PARKER;† the pedicel and lamina corresponding to "the preopercular and supra-temporal halves" and that part of the lamina below the posterior notch to the "spiracular process."

*Quadrate* (figs. 8, 20, 24, 30).—A four-sided, irregular, columnar bone, 1·8 mm. in height. The front face is free, concave from side to side, and inclined downwards and forwards; the posterior face is also free and similarly inclined, but is more irregular in form. Of the two sides, the inner is bounded by the pterygoid and the outer by the squamosal. Its antero-posterior diameter attains its greatest length in

* WILLISTON, S. F., "Primitive Reptiles," 'Journ. Morphology,' vol. 23, p. 660 (1912).

† PARKER, W. R., 'Phil. Trans.,' vol. 167, p. 571 (1877).

the middle, and diminishes towards each extremity. The lower end was probably invested with cartilage, to complete the articular surface for the articulare.

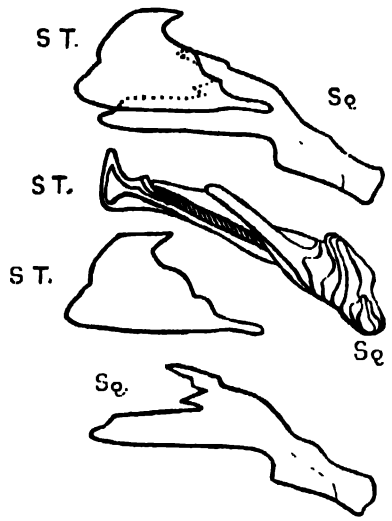



Fig. 29.




Fig. 30.

Fig. 29.—Supra-temporal and squamosal bones seen from the outer side except the second figure which represents them as looked at from below.

Fig. 30.—A. Horizontal sections (27–35) of the quadrate bone. *A*, anterior aspect; *P*, posterior aspect; *Pt.* pterygoid and *Sq.* squamosal aspects. (× 5.)

B. Horizontal sections (36–40) of the articulare.

*Supra-temporal* (figs. 1, 3, 4, 7, 8, 12, 24, 25, 29).—This is a roughly triangular lamina, thicker behind than in front, with a flat base and a truncated apex.

At the summit it articulates with the posterior process of the parietal, which is excavated to receive it and intervenes between it and the tabulare.

Below the termination of the parietal process the supra-temporal comes into close contact with the tabulare, and remains so as far as that bone descends.

Just before its termination downwards the posterior edge or back of the supra-temporal increases in thickness, and is excavated on the inner side so as to present a hook-like form in transverse section, and here it articulates with both the tabular lobe of the exoccipital and the lower end of the tabulare itself.

In front the supra-temporal extends over the outer surface of the posterior lamella of the squamosal, its lower edge resting on a step-like ledge of that bone. It completely conceals the posterior notch of the lamella as well as the vacuity in the wall of the skull behind the notch.

*Pterygoid* (figs. 7, 8, 20, 24, 31).—This long, narrow lamina or splint (5 mm. in length, 1·4 mm. in breadth, and 0·4 mm. thick), starts from the region where the pro-otic joins the posterior pillar, runs alongside the parasphenoid, and ends by curving round the anterior edge of that bone to underlie both the vomer and the palatine. From the squamosal it is separated in both specimens by the quadrate. The flank of

the splint slopes outwards and downwards, and in the direction of its length it is curved like a bow, *i.e.*, convex outwards at both extremities and concave in the middle. The upper part of the posterior end is twisted outwards at the level of the summit of the quadrate, but beyond this, the bone presents no tendency to assume the triradiate shape so common among the Stegocephalia.

*Palatine* (figs. 8, 20, 31).—The determination of this bone in all its relations is a rather difficult task, partly in consequence of the less perfect preservation of this region of the skull, a defect which is very common amongst the known specimens of Lysorophus, and partly from the absence of visible sutures, so that in the delimitation of the bone we have only general considerations to guide us.

The best preserved example of the palatine occurs on the left side of specimen 1, where it presents itself as a small more or less triangular lamina, curved outwards from base to summit and with a sinuous margin.

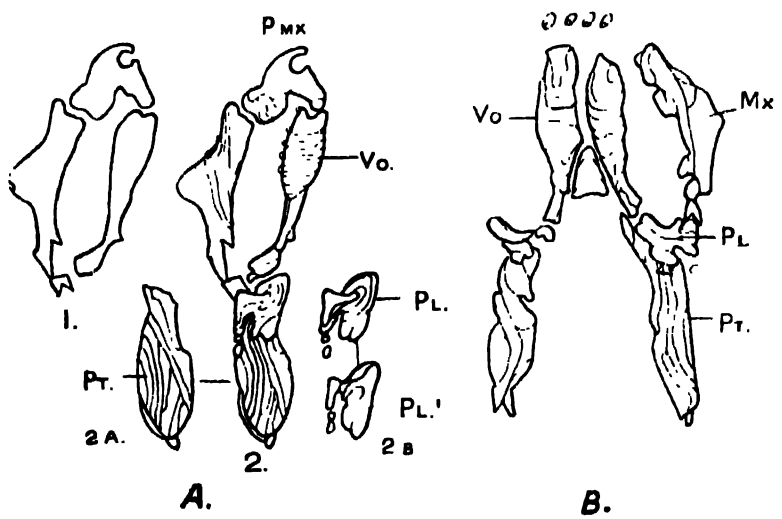



FIG. 31. - The palatine bone, showing its relations to the maxilla, vomer, and pterygoid. A. From specimen 1. (×4.) 1. Outline of premaxilla, maxilla, and vomer. 2. Superposed sections, dorsal surface. 2*A*. *Pl.*, isolated. 2*B*. *Pl.*, dorsal surface, *Pt.*, ventral surface. B. From specimen 2. (×5.)

The base continues the general course of the vomer, and lies near to its posterior termination ; the anterior end of the pterygoid underlies the base.

The lamina as it rises from the base curves outwards towards the maxilla, and at the same time assumes the form of a rounded bar which comes in contact with the posterior end of the maxilla, but whether it terminates there or not is uncertain ; for what appears to be its continuation, ending freely 0·8 mm. above the point of contact, may prove to be a part of the maxilla which has been separated from the rest by *post-mortem* dissolution.

Dr. BROOM has figured a bone* simpler in form than ours but occupying a similar position and probably representing the outwardly directed process only. This he has

* BROOM, R., *op. cit.*, p. 234, fig. 1.

identified with the palatine. An alternative explanation has been suggested to me by Mr. Goodrich who thinks it possible to regard the posterior limb of the vomer as a confluent palatine, and in that case the supposed palatine would become the transverse bone. The presence of so primitive a bone as the transverse would be quite consistent with the general character of the skull.

The additional information afforded by sections renders possible another interpretation by which the palatine nature of the bone is retained, for its base is found to occupy its proper place as the middle member of the pterygoid vomer series, while the bone figured by Dr. Broom, if it corresponds, as seems probable, with our rod-like process, is an outgrowth from it, developed to meet the need of the maxilla for support.

The *Vomers* (figs. 7, 20, 31, 32).—These are a pair of slender bones which descend backwards from the præmaxillæ to the anterior termination of the parasphenoid and the pterygoid.

The dentigerous outer border describes a graceful curve, which at first runs nearly parallel with the arc of the premaxillæ, but as it continues backwards it bends towards the middle line till it nearly completes an ellipse, it then broadens out again just in front of the anterior end of the parasphenoid and runs obliquely outwards to meet the palatine and pterygoid.

The original curve is best preserved in specimen 2; in specimen 1 a downward pressure seems to have separated the vomers so that they do not approach so closely behind, and the "waist" of the curve is enlarged.

From the dentigerous border a thin palatal lamina extends towards the middle line where it meets its fellow in a sagittal suture. The lamina is of uniform thickness (0·2 mm.) and there is no thickening next the sagittal suture.

The internal nares cannot have been situated between these bones, but must have opened outside them in the vacuity bounded by the maxilla on one side, the vomer on the other, and the palatine behind.

The length of the vomer in specimen 1 is 6 mm.; in specimen 2, 4·5 mm.

Each vomer bears nine or ten simple conical teeth, from 0·6 mm. to 1 mm. in length. They are attached to the inner side of a thickened outer border.

*Premaxillæ* (figs. 1, 2, 5–8, 20, 31–33).—These two small bones present, taken together, a bow-shaped outline in front. They are less badly preserved in specimen 1 than specimen 2. Behind they extend backwards for 2 mm., as measured along the middle line, beyond the dentigerous margin to form a thin palatal plate, which articulates with the anterior margin of the vomers. They rise in front in a short vertical wall, 0·5 mm. in height, their total height being 1·3 mm.

Measured along the arc up to its suture with the maxillæ the left premaxilla of specimen 2 is 2·5 mm. in length. The teeth, five in number on each side, are sharply pointed simple cones 0·8 mm. to 0·9 mm. in length and about 0·3 mm. to 0·4 mm. in diameter at the base.

*Maxilla* (figs. 8, 18, 20, 31, 32).—This bone continues the arc of the premaxilla,

but with a greatly diminished curvature, and, bending slightly inwards towards its termination, it gives to the upper jaw a rather elliptical outline.

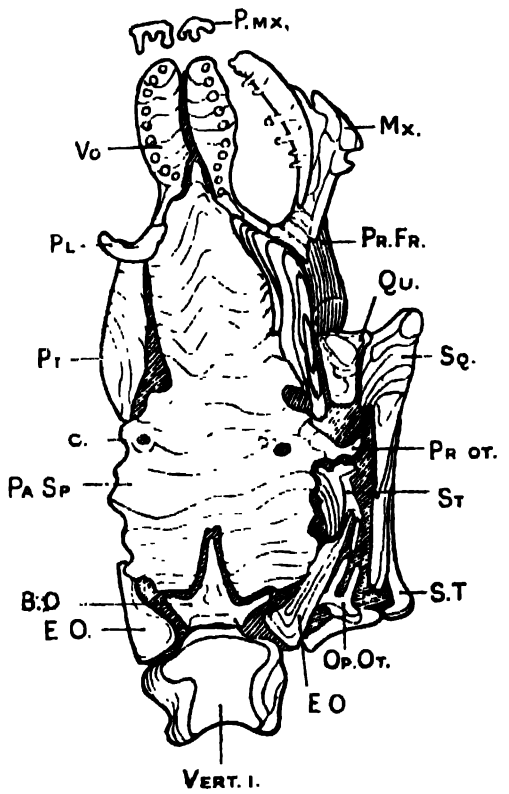



Fig. 32.

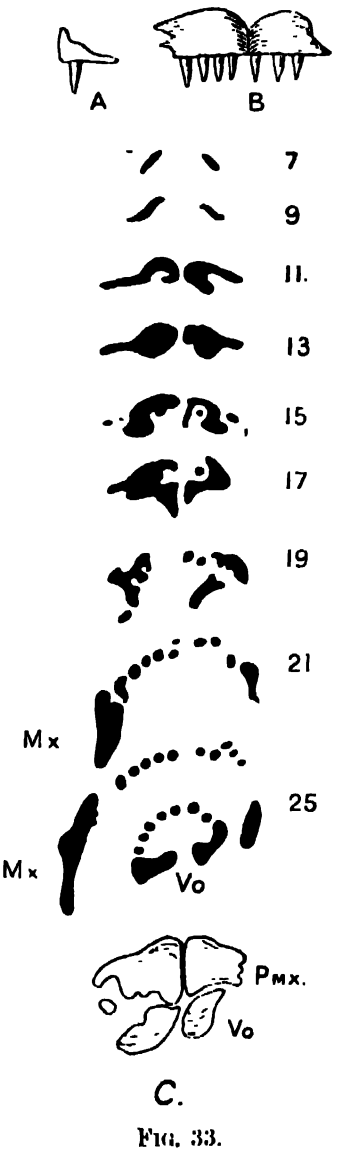



Fig. 33.

Fig. 32.—Ventral surface of the skull (specimen 2). (× 5.)

Fig. 33.—Premaxilla (specimen 1). A. The premaxillæ, vertical longitudinal section. B. Front view; 7 to 25, horizontal sections in series. C. Dorsal view of the premaxillæ and anterior end of the vomers built up from horizontal sections. (× 4.)

The body of the bone is a thin, vertical lamella, very imperfectly preserved, 1·8 mm. in height, 4·5 mm. in length, and about 0·4 mm. in thickness. The teeth are borne on the inner margin, and there is no indication of a palatal plate. The outer lower edge, near the middle of its course, is produced outwards into a rounded shelf, the base of an ascending peg-like process, which articulates by its inner face with the descending process of the prefrontal. By the union of these two processes,

an annular band or very short tube is formed on the side of the face, with its axis running parallel to the length of the skull. The ring is not, however, quite complete: it is interrupted on the inner side above by a gap, where the wall of the maxilla which bounds it on the inner side fails to reach the inner margin of the prefrontal.

This remarkable feature recalls in some respects the channel for the tentacle in Ichthyophis, as described by the SARASINS,* but a detailed comparison fails to discover any real resemblance beyond a general similarity in position.

Its lumen was evidently seen by WILLISTON, who describes a narrow space between the maxilla and prefrontal, and suggests that it was occupied by the eye. BROOM† does not accept this interpretation, and is inclined to think that it lodged some other sensory organ. He adds, after discussing the position of the nasal openings, ". . . it is impossible to be quite sure whether the bridge of bone which connects the prefrontal with the maxilla is a part of the prefrontal, or a part of the maxilla, or a small independent bone."

Our sections show, as we have seen, that the bridge is composed of (1) the descending process of the prefrontal, and (2) an ascending process, which we have attributed to the maxilla. I am not, however, without a lingering doubt on the latter point (2), for, in neither of the two cases in which the bridge is preserved, *i.e.*, on the left side of specimen 1 and the right side of specimen 2, have I been able to trace the ascending process into continuity with the shelf-like process of the maxilla; indeed, these two are separated from each other by a slight interval. If this represents a suture, then the ascending process must be an independent bone, perhaps the turbinal of the SARASINS (lacrimal of HUXLEY). The facial ring or tube would then be a narial passage running outside the wall of the maxilla, which it would have to cross in order to open between the maxilla and the vomer.

Appearances, however, suggest a fracture rather than a suture. The shelf-like process is very thin: where the ascending process comes into closest approximation to it no more than 0·1 mm. in thickness. Under the pressure to which both our specimens have been subjected, as their distortion bears witness, the fracture of so fragile a connexion would seem almost inevitable.

The teeth of the maxilla possess the same characters as those of the premaxilla; the left maxilla of specimen 1 bears ten or eleven teeth, the right maxilla of specimen 2 has one or two less.

The *Lower Jaw* (figs. 2, 4, 34–37).—Almost all the accidents which accompany fossilization, and seem designed to mislead the observer, are to be met with in the lower jaw; its analysis, therefore, proved no easy task. Sutures are imitated by little "faults" with a verisimilitude so great that when their true nature is discovered perturbing doubts arise over sutures which are truly genuine. Separate bones may

* SARASIN, PAUL and FRITZ, "Forschungen auf Ceylon," vol. 2, p. 195 *et seq.*, Plates XVIII and XIX. Wiesbaden (1887–1890).

† BROOM, R., *loc. cit.*, pp. 233, 234.

be united by a growth of calcite, and single bones resolved into several by solution. Fortunately, the material for study includes three nearly complete rami and important parts of a fourth; by constant comparison of these one with another it has been possible to arive at definite, and it is to hoped, correct results. The best preserved

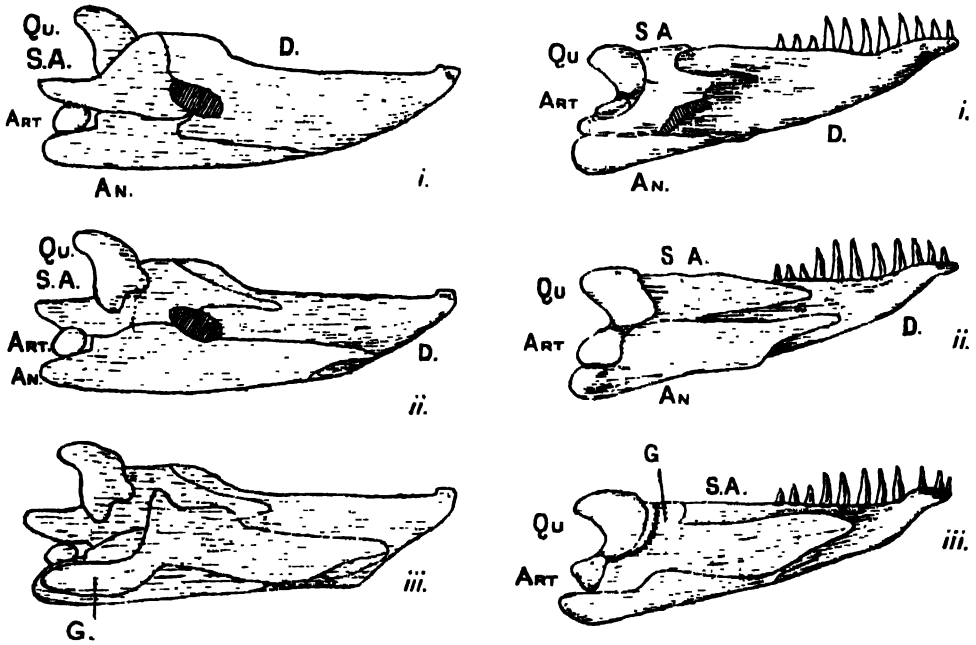



Fig. 34.—The lower jaw. On left from specimen 1. (×4.) On right from specimen 2. (×5.) i, outer; ii, inner side with goniale removed; iii, inner side with the goniale in place.

are the left ramus of specimen 1 (13·2 mm. in length and 4·2 mm. in height) and the right of specimen 2 (10·8 mm. in length and 3·4 mm. in height). These, however, suggested the presence of two bones, a splenial and pre-angular, which the right ramus of specimen 1 proves, I think, to be non-existent. This ramus (fig. 35) has been separated from its fellow, driven out of place so as to lie transverse to the axis of the skull, and squeezed open by a downward pressure which has thus revealed its structure in the clearest manner. If it is as complete as it appears to be our interpretation of the structure of the lower jaw will be relieved of all possibility of error. The left ramus of specimen 2 is very imperfect, but presents a complete row of teeth, and as it is still associated with its fellow, retaining very nearly its correct relative position, it enables us to restore the form of the lower jaw as a whole (fig. 36).

The rami diverge from a rather long and oblique symphysis at an angle of between 55° and 60°. The symphysis was evidently completed by cartilage as is shown by the facility with which the rami have been separated in some cases and displaced before the consolidation of the matrix in which they are embedded.

The *Articulare* (fig. 30, *B*) is a small irregular four-sided prism with truncated upper and lower posterior angles. Its height is 1 mm.; it is seated on the angulare and embraced on one side by that bone and on the other by the goniale. When I

previously referred to it elsewhere* as "a comparatively large and important bone," I was unaware that the quadrate which is in close contact with it in specimen 2 is in fact a separate element.

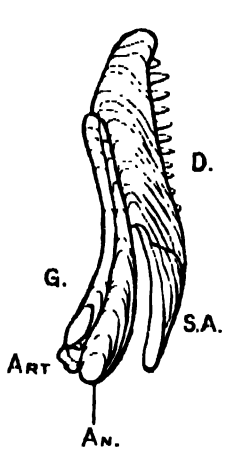



FIG. 35

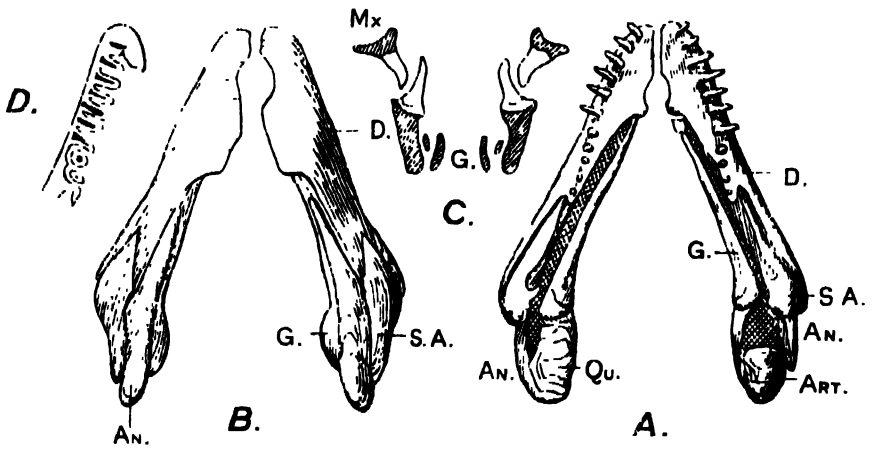



FIG. 36.

FIG. 35. Right ramus of lower jaw (specimen 1) squeezed open by vertical pressure, seen from below. (×4.)

FIG. 36.—Lower jaw (specimen 2). A. Seen from above. B. From below. (×5.) C. Transverse section through the lower jaw and maxilla of specimen 1 to show the implantation of the teeth. D. Horizontal section through the dentary of specimen 1 showing the base of the teeth. (C and D, ×4.)

The *Surangulare* (fig. 37) is a fairly long splint, thickened behind and produced there into a hook-like process on the inner face, probably for attachment of the masseter muscle.

The posterior margin descends as a vertical wall which rests at the base on the angulare. In specimen 2 the base is produced backwards to form along with the angulare a rather long post-articular process. This is shown also in the figure which BROOM gives of the lower jaw. In specimen 1 the angular and surangular elements of the process have been pushed apart from each other; a fortunate accident, affording confirmatory evidence of the precise delimitation of these bones, which might otherwise have been in doubt. The surangulare and the dentary form together a low coronoid process, no doubt for the attachment of the temporal muscle.

The *Angulare* (fig. 37) is a rather thick bone, where it forms the angle of the ramus, but is continued upwards and forwards as a thin lamella lying between the dentary and the goniale and extending as far or almost as far as the goniale to the front. It is excavated on the medial side behind and below to receive the postero-inferior termination of the goniale.

The *Goniale* (fig. 37).—This long splint articulates behind and below with the angulare; it is continued forwards as far as the symphysial margin of the dentary.

* In BROOM, *op. cit.*, p. 239.

Just above and in front of its articulation with the angulare the lamella is abruptly truncated behind and the truncated edge is thickened; it rises in a steep wall corresponding to that of the surangulare on the opposite side of the ramus. Near its foot this wall is perforated obliquely by a small foramen, probably the foramen *pro chorda tympani*.

As already mentioned, the posterior extremity of the goniale is applied to the inner side of the articulare.

So far as I can make out a splenial bone is not present. I fancy that the bone which BROOM indicates in his figure of the lower jaw under this name, must be either a part of the angulare or the continuation of the goniale (pre-articulare). If it were really splenial then the pre-articulare shown in the section given by BROOM along the line *a a* of his figure would be splenial also, for the only region where the bone which I have identified as goniale could be resolved into two elements lies considerably behind this line. In this region some of my sections might possibly be taken to represent both elements—splenial and goniale. Indeed, this was the interpretation which at first commended itself to me, but it is in no way confirmed by an examination of the right ramus of specimen 1. On the contrary, this strongly supports the view that of these two bones, splenial and goniale, only one is present, not both. Which of the two it is may be a matter of opinion, but the bone extends so far backwards, almost to the posterior extremity of the jaw, that the presumption is in favour of the goniale.

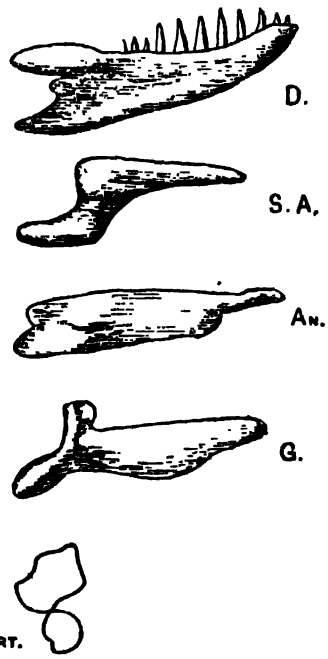



FIG. 37. The bones of the lower jaw, specimen 2. (×5.)

The *Dentary* (fig. 37) is a large splint-like bone 8 mm. in length, thickened at the distal end, which is excavated by a deep groove for Meckel's cartilage, and expanded above into a horizontal ledge which bears the teeth. It is sutured with the surangulare and overlaps both that bone and the angulare for a great part of their length. In front and below it is in contact with the goniale. Where it meets the surangulare near the angulare is a small external mandibular foramen.

The *Teeth*.- The teeth are simple, hollow, sharply pointed, elongate cones. They are slightly curved (figs. 34, 36), and when attention is confined to horizontal sections they appear to be rather suddenly bent near the base into parallelism with the surface of the bone from which they spring. This would suggest a comparison with the teeth of some Urodeles, such, for instance, as Megalobatrachus, but with this difference, that the opening of the root is not, as it is in that genus, turned away from the outer margin of the dentigerous bone, but in the contrary direction.

Further, when vertical sections are constructed they present no trace of such a suggested bending, the tooth is typically acrodont, and the bending must be interpreted as an elongation of the base (fig. 36. *C*). The teeth are, in fact, more like those of a fish, such as Amia, than a Urodele.

In one instance the tooth appears to have been folded near the base as in some of the simpler Stegocephalian teeth and the teeth of the existing Ceratophrys; such at least appears to be the only possible explanation of such a section as that shown near the letter *D* in Section 27, Plate 70, from the right dentary of specimen 2. Similar but less definite foldings are presented by the roots of all the teeth preserved in the left dentary of the same specimen (Section 29, Plate 70). In order to determine whether the length of the teeth in a series is distributed according to any law the measurements were made which are given in the following Table :—

LENGTH of the Teeth Arranged in Order from before Backwards.

| | 1. | 2. | 3. | 4. | 5. | 6. | 7. | 8. | 9. | 10. | 11. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Pmx., L., specimen 1 | 0·9 | 0·9 | 0·8 | 0·8 | 0·8 | | | | | | |
| Mx., L., specimen 1 | 0·6 | 0·6 | 0·7 | 0·6 | 0·8 | 0·8 | 0·8 | 0·7 | 0·2 | 0·2 | |
| Mx., R., „ 2 | 0·6 | 0·8 | 0·8 | ? | 0·6 | 0·4 | 0·4 | 0·6 | | | |
| Vo., L., „ 1 | 0·8 | 0·6 | 0·7 | 0·7 | 0·6 | 0·4 | 0·2 | 0·2 | 0·5 | | |
| Vo., L., „ 2 | 1·0 | 1·0 | 0·8 | 0·8 | 1·0 | 1·0 | 0·6 | 0·2 | 0·6 | | |
| D., L. „ 1 | 0·9 | 1·1 | 1·3 | 1·3 | 1·5 | 1·5 | 1·4 | 1·2 | 1·2 | 1·0 | 0·9 |
| D., R., „ 2 | 0·4 | 1·0 | 1·2 | 1·2 | 1·2 | 1·2 | 1·0 | 1·0 | 0·6 | 0·6 | |

They are not all of equal value; those taken from specimen 1 are, on the whole, more trustworthy than those of specimen 2; the maxilla and its teeth are badly preserved in specimen 2, and, of the premaxilla, only a trace remains.

It will be seen that the dentary, the only dentigerous bone in the lower jaw of Lysorophus, bears from 10 to 11 teeth, which are generally larger than those of the upper jaw, and that the longest of them are situated in the middle part of the series, the shortest at the ends. WILLISTON found 12 teeth in the specimen described by him.

### *The Visceral Arches.*

The *Hyoid* (figs. 2, 11, 38, 39, 40).—In both specimens the hyoid bones are differently preserved on different sides. In specimen 1 the left hyoid, and in specimen 2 the right, seem to retain very nearly their original form and position. The right hyoid of specimen 1 has been displaced; it lies on its side, and has been flattened out by compression. It was probably a displaced and deformed hyoid that BROILI mistook for a gular plate.

The well preserved examples both present similar characters with slight differences; they consist of a hypohyal and a ceratohyal, the two elements together forming a bone which, in specimen 1, looks very like a lower jaw with a well-marked horizontal

and vertical ramus. In specimen 2 the constituent elements are more sharply distinguished from each other. In this the hypohyal is a thin bar, 2·0 mm. in length and 2 mm. in height, straight on the mediad face, curved inwards from side to side on the outer face; it is thickened above, and gives off an uncinate process, which points backwards towards the middle line. The ceratohyal is a large lamellar bone, gently curved from above downwards towards the middle line. It is 2·8 mm. in height and 4·5 mm. in length at the summit, but becomes shorter as it descends by a forward sweep of its posterior edge till it is reduced to 2 mm. in length. Narrow in the middle, it thickens out towards both extremities; in front, for the greater part of its height; behind, directly towards the summit, where it forms what appears to be an articular head, rising 0·6 mm. above the middle region and 0·4 mm. above the anterior end. On its posterior face the head is excavated into a cup-like hollow.

*First Branchial Arch* (figs. 2, 38, 39, 40).—This includes a ceratobranchial

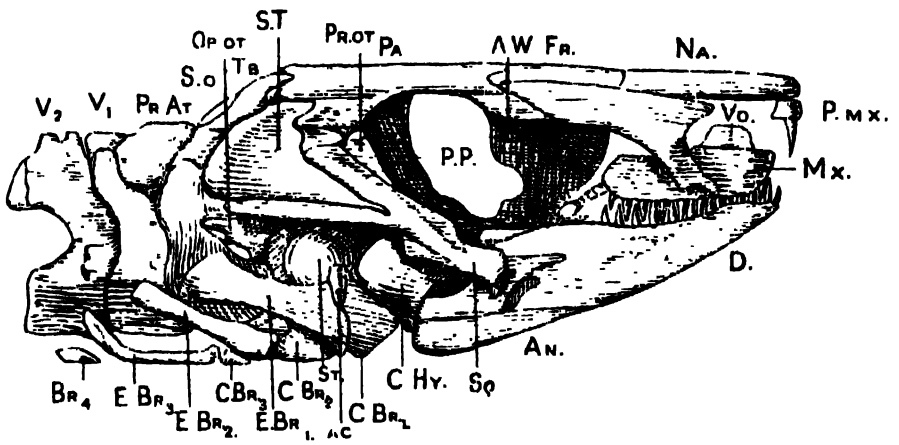



Fig. 38.—The skull with the visceral arches. (×5.)

and epibranchial member. The two together form a large lamella, curved inwards like the side of a boat, 9 mm. in length, measured along the chord of the arc.

The ceratobranchials of each side, 5 mm. in length and 2 mm. in height, meet with thickened ends in the middle line. The ends bound a concave space in front, which, during life, possibly received the posterior end of a cartilaginous basi-hyal.

As the ceratobranchials pass backwards to their union with the epibranchials, they increase in vertical height, and at the junction on the outside is a little ossicle, which lies along the articular edge from base to summit. This seems to be an accidental bone (*ac.*, figs. 38, 39).

The epibranchial resembles the ceratobranchial, but is shorter, 4 mm. in length, and its posterior end does not approach the middle line.

The first branchial arch of specimen 1 is similar but larger, 11·5 mm. in length, straighter and less incurved. Like the hyoid, it resembles a lower jaw, and the

ascending ramus lies inside and a little behind that of the hyoid on the side of the skull.

The *second branchial arch* resembles the first, but is less lamellar and more rod-like at the extremities; the ceratobranchial is 4·4 mm. and the epibranchial 4 mm. in length; towards their articulation with each other they are flattened out in a horizontal plane, possibly as the result of rock pressure.

The *third branchial arch* is similar to the second; the ceratobranchial and the epibranchial are each 4 mm. in length. The epibranchial and the posterior part of the ceratobranchial are much flattened out in a horizontal plane. Although of approximately the same length, these are much feebler bones than those of the second arch. The third ceratobranchials nearly meet in the middle line. Lying between them is a straight minute rod of bone, 1·8 mm. long and 0·4 mm. in diameter, which extends along the middle line, and apparently represents a basi-branchial element. The general character of the arches strongly suggests that, originally, an unbroken series of basi-branchials existed, and completed the branchial skeleton in the middle line; it is possible even that they were more or less ossified, but have subsequently been destroyed by decay and solution.

A *fourth branchial arch* seems to be represented by a train of fragments, which arises within the third arch and runs parallel with it and beyond it as far as the third vertebra.

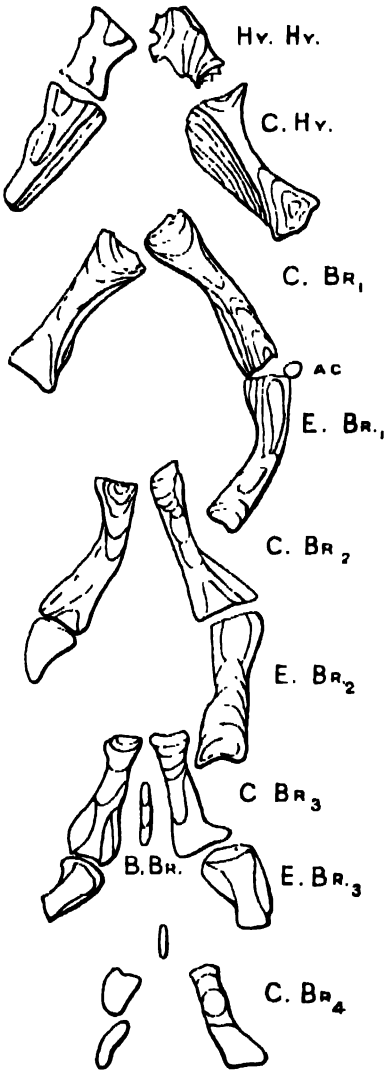



FIG. 39.—The Hyoid and Branchial Arches. *Hy.Hy.*, hypohyal; *C.Hy.*, cerato-hyal; *C.Br.*, cerato-branchial; *E.Br.*, epi-branchial; *B.Br.*, basi-branchial. (×5.) *ac*, an accessory ossicle.

The most remarkable character of the hyoid and first branchial arch is their compressed plate-like form; in this, as in the form of the other branchial arches also, offering a striking contrast to Polypterus; they strongly recall Megalobatrachus with the difference that they do not lie flat or parallel to the ventral surface but make a close approach to the vertical; the second branchial arch is even more similar to that of Megalobatrachus. The hyoid both by its form and position finds its nearest parallel among the bony fishes; an epihyal, however, does not enter into its composition.

The *Vertebral Column.*—For the purpose of description it will be convenient to

distinguish the first four vertebræ, which lie in front of the shoulder girdle, as "cervical" and all those behind these, as far as the sacrum, as dorsal vertebræ. Our material may thus be said to include the first and second cervical vertebræ and a series of four dorsal vertebræ in specimen 1, and in specimen 2 all the cervical, including the pro-atlas, and as well two dorsal vertebræ very remote from the head. These were all cut in horizontal sections, except the two last named which were cut transversely.

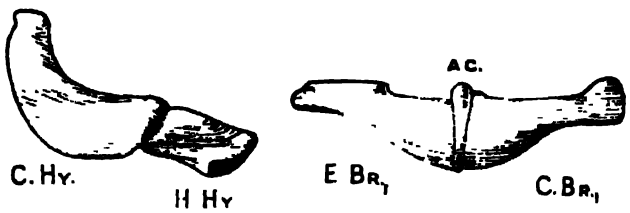



Fig. 40.—i. The hyoid bones from specimen 1. (×4.) ii. The first branchial arch from specimen 2. (×5.)

*Dorsal Vertebræ.*—The centrum is cylindrical, but with two deep depressions on the sides, one, the smaller above the middle and the other the larger below it, so that a transverse section through this region presents the form shown in fig. 43, Nos. 7 and 27.

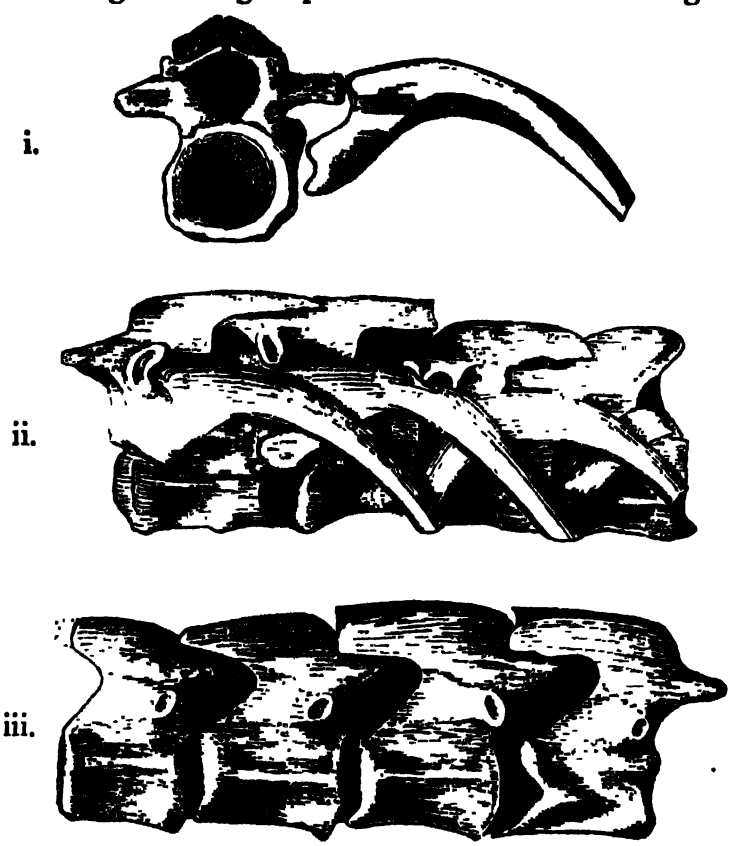



Fig. 41.—Dorsal vertebra. i. Seen from in front and showing the rib placed at right angles to the axis of the vertebra. ii. Lateral view (left side) with the ribs in the position they occupy in the fossil. iii. Lateral view (right side) without the ribs. (×4.)

It is deeply amphicœlous and perforate. Its breadth is approximately the same as its length, viz., 5·5 mm. to 6 mm. in specimen 1 which is 4·5 mm. to 5 mm. in height; in specimen 2 the height is 3·6 mm. and the length 4 mm., but in this case not only is the specimen itself smaller but the vertebræ measured lie nearer the head.

The neural arch consists of a pair of lateral elements which appear to have been united with the centrum below and with each other above by synchondrosis. Its height is about the same as that of the centrum; thus in a vertebra 10 mm. in height, the arch measured 5 mm.

The piers of the arch are produced over their anterior half into a stout transverse process. The root of the process is strictly confined to the arch and does not extend downwards over the centrum.

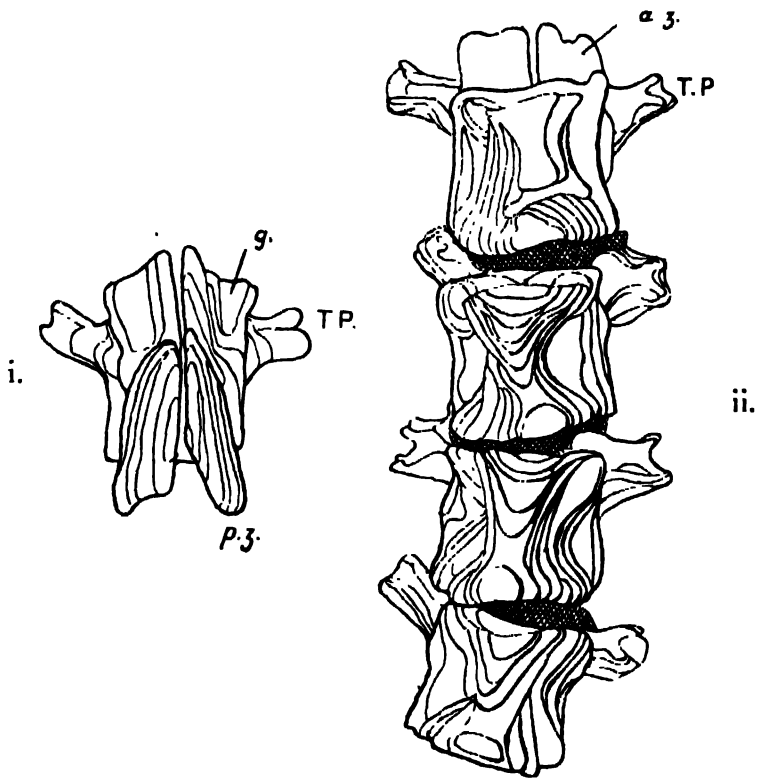



Fig. 42.—i. Dorsal vertebræ of specimen 1 seen from above and built up of superposed sections. (× 4.) ii. Dorsal vertebra of specimen 1 seen from below. (× 4.) T.P., transverse process; *a.z.*, prezygapophysis; *p.z.*, post-zygapophysis; *g.*, groove in prezygapophysis to receive post-zygapophysis.

Behind the transverse process the sides of the arch are rather deeply excavated to form the anterior margin of the intervertebral foramina.

Immediately above the root of the transverse process the sides of the arch rapidly approach each other, roofing over the spinal canal, and extend forwards as a pair of horizontal plates—the anterior zygapophyses—which project a considerable distance beyond the face of the centrum. Each plate bears a wide and shallow groove for articulation with the posterior zygapophyses.

Behind this region the sides of the arch again ascend and rather steeply, forming a vault, closed in front, and resembling the bow of an inverted boat, but without a keel, for a neural spine is not present. The sides of the bow broaden out behind in two diverging wings which, extending beyond the posterior end of the centrum, articulate with the prezygapophyses and ensheath the "bow" of the succeeding arch.

The transverse processes look outwards and slightly forwards. A little pit-like depression in front of the root and another behind suggest the existence of a foramen, of which however there are no other signs. The ends of the processes are excavated for the attachment of articular cartilage.

The whole inner and outer surface of the centrum, including the central perforation, is formed by a layer of dense bone, which is perforated by minute vascular pores, very regularly arranged. Within this layer the structure is cancellous, but at the same time, as shown by transverse sections (fig. 43, Nos. 7, 27), definitely radiate. The chief radii

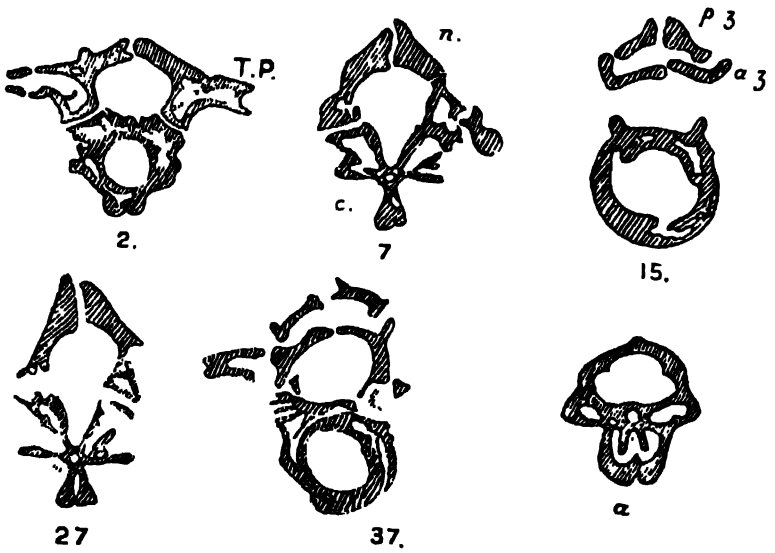



Fig. 43, 2 to 37.—Vertical transverse sections of two dorsal vertebræ of Lysorophus. *a*. Of a dorsal vertebra of Crypto-branchus; *c*. Centrum; *n*. Neural arch. (×5.)

are six in number, two lateral and horizontal, two directed upwards and outwards, and two downwards. The descending rays are closely approximated and almost fuse into one, the others make an angle of about 60° with each other. Lysorophus is not the only Amphibian which possesses this piscine character; it is also met with in Cryptobranchus and possibly other Urodeles. In Cryptobranchus also the dense investing layer of bone is perforated by minute pores just as in Lysorophus. It should be added that between the two ascending radii the floor of the spinal canal descends to form a deep pit; and it is in the intervals between adjacent radii that the upper and lower lateral depressions of the centrum are situated. In these details Lysorophus presents a surprising resemblance to some of the bony fishes, such as the Tunny.

As they approach the cervical region the dorsal vertebræ undergo slight changes of form and the transverse processes no longer look forwards but directly outwards. They are associated with stout two-headed ribs, as also is the fourth cervical vertebra.

*Cervical Vertebræ.*—As we pass from the dorsal series forwards slight modifications set in, which become increasingly marked as we proceed. The third and fourth vertebræ closely resemble the dorsal, differing only in minor details. They are smaller as a whole,* and the height of the arch (3 mm.) exceeds that of the centrum (2 mm. in specimen 2). In the dorsal vertebræ the face of the centrum is larger than the lumen of the spinal canal; in the cervical this relation is reversed.

The zygapophyses are less completely differentiated, so that the articulation assumes still more the character of an ensheathment. At the same time the crest of the arch, formed by the approximation of its sides to the exclusion of the spinal canal beneath, increases in height and diminishes in length.

The transverse processes of the fourth vertebra, as of the dorsal vertebræ immediately succeeding it, are not directed forwards as in the dorsal vertebræ just described, but simply outwards. They are still articulate, however, with two headed ribs. In the second and third vertebræ the transverse processes look outwards and backwards, and the associated ribs, no longer double-headed, are short and slender; thus, in the third vertebra they are 5 mm. in length and less than 3 mm. in the second.

In the *second vertebra* the height of the arch has increased to 3·6 mm., the posterior wings have become shorter, and the crest of the arch is less than half the length of the vertebra behind it. The region of the anterior zygapophyses is still well expressed however by a hood-like extension forwards, which is ensheathed by the arch of the first vertebra.

The *first vertebra* is more profoundly modified. The crest of the arch is now represented by two little cylindrical tubercles, one to each lateral moiety; the transverse process is a mere tubercle, and there are no ribs.

In front the arch no longer projects forwards in definite zygapophyses, or perhaps it should rather be said that these have been shortened to their roots. The piers of the arch are applied in front to the posterior edge of the pillars of the exoccipitals.

"*Pro-atlas.*"—The forward slope of the occiput and the backward slope of the roof of the arch of the first vertebra produce a V-shaped trough, and into this is neatly fitted the paired pro-atlas, which rides like a saddle across the "neck."

The pro-atlas resembles the vault of a vertebral arch, but turned about, *i.e.*, with what would be the anterior face of the arch looking backwards. This is a consequence of its adaptation to the surfaces with which it articulates, the occipital being much

* Thus in specimen 1 we have the following measurements for the centrum :—

| | Breadth. | Length. | Height. |
|---|---|---|---|
| Dorsal . . . . . | 5·4 | 5·5 | 4·5 |
| Cervical II . . . . . | 3·5 | 3·4 | 3·25 |

broader than the vertebral surface. Its posterior face is moulded on to the face of the first vertebral arch, and its posterior extremity enters the space between the two little tubercles which form the crest of this arch. Its anterior face is applied to the ascending part of the supra-occipital and the medial half of the lamina of the exoccipital. This lamina bears a groove which corresponds with the edge of the surface of articulation.

The two elements of the pro-atlas are articulated together over a broad surface, but readily fall apart, from which we may conclude that they were originally united by synchondrosis. Like so many other paired elements of the skeleton, they are far from being symmetrical one to another on each side of a median plane. The right half is much thicker than the left, and provided more than its share to the articulation with the back of the skull.

Williston, who at first recognised the presence of a pro-atlas,* afterwards stated that "the supposed pro-atlas described by Case and myself is merely the arch of the so-called atlas."† That so acute an observer should have been misled on this point will surprise no one who is familiar with Lysorophus; without the aid of sections it would be next to impossible to arrive at a certain conclusion: these, however, show in the clearest manner that the first vertebra possesses its own arch, and that the pro-atlas is without a visible centrum.

*The Centrum of the First Vertebra.*

Next to the parasphenoid this and the condyles are perhaps the most amphibian structures in the skeleton. It is opisthocœlous and imperforate, slightly broader than the succeeding vertebra, and higher behind (2 mm.) than in front (1·2 mm.), the upper surface being scooped out by a shallow groove, 4 mm. in breadth and 3 mm. in length, which descends forwards. The hollow cone which forms the anterior face of the other vertebræ is here replaced by a cylindrical convexity, which corresponds to the "odontoid" of the Amphibia, and plays against the nearly flat posterior surface of the basi-occipital. It is composed of slightly denser tissue than the rest of the bone.

On each side of the "odontoid" is a little flange forming the bottom of a shallow recess, which receives the back of the heel of the exoccipital bones.

The condyle of the skull might thus be regarded as tripartite, though the parts are so far from being fused into a single structure that it would seem more appropriate to speak of three condyles than of one. But even if we admit the term "tripartite" as legitimate, it by no means follows that the articulation is in any sense reptilian. It offers indeed a direct contrast to the reptilian articulation for the exoccipital facets look downwards and inwards in Lysorophus instead of outwards as in reptiles, and this difference is directly correlated with another. If, broadly speaking, we may compare the condylar articulation to a ball-and-socket joint, then

* Williston, 'Biol. Bull.,' vol. 15, p. 229 (1908).

† Williston, 'J. Geol.,' vol. 18, p. 600 (1910).

the occipital condyle of a reptile plainly corresponds to the "ball"; in Lysorophus, on the contrary, it supplies the socket, or if we could apply such terms to an articulation we might say that in Lysorophus the joint is procœlous, in the Reptiles opisthocœlous. Thus in this essential particular Lysorophus offers a direct contrast to the Reptilia and it is easy to understand how such an articulation would pass by a reduction of the basi-occipital into that which now characterizes the existent Amphibia. But in Lysorophus the articulation of the skull with the vertebral column is not confined to the centrum of the first vertebra; it extends to the piers of the arch of this vertebra and to the pro-atlas. Such a close association of the whole vertebral front with the back of the skull is a character which irresistibly recalls certain fishes among the Teleosts, in which the first vertebra is similarly plastered on to the occiput. It seems to point to a time when, as my friend Mr. GOODRICH remarks, the limit between skull and vertebræ was in a state of flux.

*Caudal Vertebræ.*—Unfortunately these are not represented in my sections. By no means anticipating that the specimens would yield so much detailed information, I restricted my attention to the head and its vicinity. Had I known the full value of the material placed in my hands, I should have prepared sections of the entire skeleton. My regret is tempered, however, by the fact that the caudal vertebræ have been described by WILLISTON who asserts that they are without [free] chevrons, and thus definitely Amphibian. They are said to be 17 in number and without ribs or diapophyses.

The *Ribs* (figs. 40, 44).—In all but those of the second and third vertebræ the ribs are two-headed, the tubercular process extending about 4 mm. or 5 mm. beyond the capitulum. All the ribs have suffered some displacement, and are now folded back against the sides of the vertebral column, round which they curl to cross one another below on the ventral surface. This singular disposition has been noticed already by CASE in his specimens. It is probably connected with the fact that the serpentine body is always found closely coiled up; at the same time it suggests that the ribs possessed great freedom of movement and whatever further may be implied by this. The tuberculum lies close to the transverse process, usually just beneath it; the capitulum against the side of the centrum which offers no definite facet for its articulation. Where the rib bends away from the capitulum it is compressed from side to side, so that a transverse section is about twice as high (2 mm.) as broad

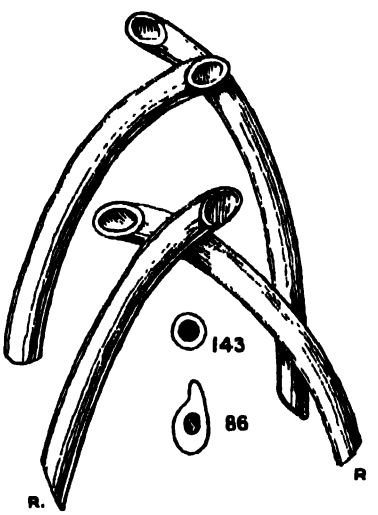



FIG. 44.—*R. R.*, ribs crossing each other below the centra of the vertebræ; 86, oblique section through a rib about 1 mm. beyond the tuberculum; 143, transverse section through the same rib near its distal termination. (All from specimen 1; × 4.)

(1 mm. to 1·25 mm.). It becomes rounder as it proceeds and maintains a diameter of 1·4 mm. for a considerable distance; later it is hollowed out in some cases on one side leaving a ridge to form the posterior edge. The ribs are hollow and the cavity they enclose enlarges by thinning of the wall as they approach their termination. In specimen 1, so far as I can trace them, they are about 11 mm. in length measured along the chord, and 15 mm. along the arc.

*Appendicular Skeleton.*

*Shoulder Girdle* (figs. 1 and 2). - The shoulder girdle lies outside the ribs and partly below them. There has evidently been much displacement not far from the third and fourth vertebræ. As in the Urodeles, the dorsal region is not represented by bone.

The *scapula* is a short narrow triangular plate, 2·6 mm. in length; at one corner, now turned forward as a result of displacement, it bears a concave surface, which appears to represent part of the glenoid cavity.

The *clavicle* is a long slender curved rod; its upturned posterior end lies just behind the scapula, thence it curves under that bone, touching it below the articular surface, and runs obliquely downwards and forwards, to end beneath the first rib. At its termination is an elongated triangular plate, lying flat in the ventral plane. Whether this is to be regarded as an expansion of the clavicle or an independent element, there is nothing to show.

A small elongate splint-like bone (*s*, fig. 2) lies in front of the clavicle near the vertebral column, and looks as though it belonged to the shoulder girdle. A cleithrum may possibly be represented either by it or the bone we have assigned to the clavicle.

*Fore Limb.*—The scattered members of the fore limb lie along a line perpendicular to the direction of the vertebral column.

*Humerus.*- This is represented by a cylindrical shaft, 3·6 mm. in length, narrowest in the middle, widest at the extremities, which are more or less cup-shaped, owing to the disappearance of the cartilage by which they were originally completed.

A cartilaginous extremity is very characteristic of Urodele limb bones.

The distal end of the humerus is distinguished from the proximal by a rounded swelling on one side.

The long axes of the articular ends lie at right angles to each other, as is shown by the following measurements :—

Breadth of articular end measured from—

| | Above downwards. | From side to side. |
|---|---|---|
| Proximal end . . . . | 1·2 m.m. | 0·8 m.m. |
| Distal end . . . . . | 0·8 „ | 1·4 „ |

This is a feature commoner among Mammals and Urodeles than among Reptiles.

*Radius.*—The radius is a straight slender rod, 2·2 mm. in length, and concave at

both ends. It lies on the pre-axial side of the humerus, and points in the same direction as the humerus, but is separated from it by a considerable interval.

The *ulna* is also a slender rod, of about the same length as the radius, but rather strongly curved. It is post-axial, with its proximal articulation near the distal end of the humerus; it has been driven apart from the radius, and lies obliquely to the plane of the sections.

There is no trace of carpal bones, which, as is usual among modern Urodeles, were in all probability cartilaginous.

*Metacarpals.*—The metacarpals of two digits are preserved as simple rounded rods, lying side by side close together, oblique to the plane of the sections. One is slightly longer (1·4 mm.) than the other (1·2 mm.).

Miss MARIAN FINNEY* examined 200 nodules, containing remains of Lysorophus, in search of limb bones, and found 15 examples, which included some femurs, tibias, and fibulas, two metatarsals, and two phalanges.

Presuming that these determinations, which depend entirely on the form of the bones, are correct, it would follow that Lysorophus was provided with both fore and hind limbs, and, from Miss FINNEY's observations, it is possible to make some comparison of their length. Thus the femur was found to measure 10·5 mm., while the humerus in our specimen is 3·6 mm. long; similarly, the tibia and fibula are 5 mm. and the radius and ulna 1·8 mm. in length. Unfortunately, nothing is known of the size of the head with which Miss FINNEY's specimens were once associated, but she mentions the presence of part of a lower jaw, bearing 11 teeth and measuring 8 mm. in length. In the specimen which furnished the fore limb of our description, the dentigerous part of the dentary, measured as far as the 11th tooth, is only 4·6 mm. in length; hence we may conclude that heads, almost twice as long as that of our specimen 2, may have accompanied the bones of the hind limb described by Miss FINNEY.

That such heads exist is beyond doubt; Dr. WATSON is in possession of one which is about 30 mm. in length; nearly twice the size of average specimens, as he remarks, while adding that, on this account, it may prove to belong to a different species.

If we may assume that the ratio of the length of head to limb did not vary greatly with the size of the animal, then we may obtain a rough estimate of the relative length of the femur and humerus by multiplying the length of our humerus by 2, since, as we have seen, the head associated with it is only about one-half the length of that associated with the femur. We should then have humerus 7·2 mm., femur 10·5 mm., a ratio of about 7 : 10; in a specimen of Cryptobranchus, I find it to be 7 : 9, and a similar ratio obtains for Necturus and some other forms. Thus our imperfect data at least suggest that the hind limbs of Lysorophus were longer than the fore limbs.

* FINNEY, MARIAN, "The Limbs of Lysorophus," 'Journ. Morphology,' vol. 23, pp. 664–667 (1912).

A comparison of the relative size of the fore limbs of Lysorophus, two modern Urodeles and a Branchiosaur may not be without interest. Taking the length of the head as a basis, we have the following :—

| | Head. | Hu. | Hu × 100/Head. Index. |
|---|---|---|---|
| Cryptobranchus . . . . | 40 mm. | 17 mm. | 42·5 |
| Necturus . . . . . | 42 ,, | 15 ,, | 36 |
| Lysorophus . . . . . | 16·0 ,, | 3·6 ,, | 22·5 |
| Urocordylus . . . . . | 38 ,, | 5 ,, | 13 |

Next taking the length of the humerus as a basis we have :—

| | Ra. | Index. | M.ca. | Index. |
|---|---|---|---|---|
| Cryptobranchus . . . | 9 mm. | 53 | 4 mm. | 23·5 |
| Necturus . . . . . | 8 ,, | 53 | 4 ,, | 26 |
| Lysorophus . . . . | 1·8 ,, | 50 | 1·4 ,, | 39 |
| Urocordylus . . . . | 3·5 ,, | 70 | | |

And finally with the length of the head as a basis we have :—

| | Hu + Ra + M.ca | Index |
|---|---|---|
| Cryptobranchus . . . . | 30 mm. | 75 |
| Necturus . . . . . | 27 ,, | 64 |
| Lysorophus . . . . . | 6·8 ,, | 42·5 |

The total length of the fore limb in Lysorophus cannot have been much more than one-half that of the ribs, which, as we have seen, attain a length of 15 mm.

In the light of our present knowledge, Lysorophus stands clearly revealed as a veritable but primitive Amphibian, and no less clearly as a member of the ancestral Urodeles.

Most of the characters by which it differs from existing Urodeles, are such as we might expect to find in a primitive form. The presence, for instance, of a well ossified basi-occipital and supra-occipital, the existence of a foramen for the twelfth nerve, and, possibly connected with this, the presence of a "pro-atlas"; the nature of the condylar articulation of the skull, which represents a stage still existent among the bony fishes, but long since left behind and forgotten in the history of the Amphibia; further, the presence of a separate opisthotic, large tabulares, conspicuous supra-temporal bones, a complex lower jaw, and large well ossified branchial arches.

There are other characters which appear to be peculiar, such as the mode of union of the maxilla with the palatine, and of this bone with the vomer and pterygoid, the nature of the vertebræ, and the well curved form of the long ribs. This last character Lysorophus shares with the Gymnophiona, and so far supports the view long held by distinguished naturalists, that the Gymnophiona stand in close connection

with the Urodeles; Cope considered that they were united to the more typical Urodeles by the Amphiumidæ, and the Sarasins not only shared this view but went so far as to include the Gymnophiona and the Amphiumidæ in a single group—one of the two sub-orders which constituted, according to them, the order Urodela.

If this alliance be admitted it would seem clear that the Gymnophiona must have branched off from the main stem prior to Lysorophus, for they still retain important bones, the lacrimal or lateral nasal, postfrontal or postorbital, and jugal which had already been discarded by Lysorophus in Carboniferous bones.

The breach between the Urodeles and the Anura was probably accomplished at a very early date, for all the features of the skeleton which distinguish the Urodeles are already fully expressed in Lysorophus: thus, in the skull the parasphenoid is large and characteristic, the roofing bones are distinct, there is a large prefrontal, a quadrate but no jugal nor quadrato-jugal: and the squamosal is directed forwards as in Siren, Proteus and Necturus. The presence of the tabulare recalls Proteus and Amblystoma.

In the present state of our knowledge speculations on the family history of Lysorophus would seem out of place. That its pedigree included a terrestrial ancestor which used its legs for progression on dry land would seem to be precluded by the persistence of a well-developed branchial apparatus. Its feeble limbs afford but slight ground for argument; we are not entitled to assume without further evidence, that at some ancestral stage they were more strongly developed. Our knowledge of the steps by which fins were transformed into ambulatory limbs is not advanced enough to justify dogmatism on this point; the earliest limbs may have been feeble organs adapted to progression under water.*

The closely wound coils in which the body is now disposed shows that the vertebral column was capable of freely undulating movements by which in all probability progress in the water was accomplished.

The meaning of the large ribs with their wide range of movement is not clear; it is possible that there also might have been organs of locomotion which were called into play by special circumstances.

The Dipnoi, to which we might turn for some light on the nature of the material from which the early Tetrapods were derived, are already too specialized, at least in known forms, to help us much. Dipterus, which in general plan survives in the existing Ceratodus, presents a parasphenoid which by its breadth makes the nearest approach to the Urodeles; but the peculiarity of its dentition precludes closer comparison. Our knowledge of the palæozoic lung-bearing fishes must be much more extensive before we can speculate profitably on this question, but in any case the

* For an interesting hypothesis on the origin of the Tetrapod limbs, see R. Broom, "On the Origin of the Cheiropterygium," 'Bull. Amer. Mus. Nat. Hist.,' vol. 32, pp. 459–461 (1913), and B. Petronievics, "Note on the Pectoral Fin of Eusthenopteron," 'Ann. and Mag. Nat. Hist,' Ser. 9, vol. ii, pp. 471-476 (1918) (includes an account of the literature).

Dipnoi proper seem to be excluded from the direct line of Amphibian descent by the nature of their ribs.

Dr. WATSON has arrived at important conclusions on the phylogeny of some orders of the Stegocephalia, which at present are only published in abstract. He concludes that in the general course of evolution as illustrated by this group there is a gradual regression and final disappearance from the skull of the foramen for the twelfth nerve, an increase in the size of the interpterygoid vacuities and of the parasphenoidal rostrum, a replacement of the basi-pterygoid processes of the basi-sphenoid by expansions of the parasphenoid and exoccipital, a reduction and final disappearance of the basi-occipital, basi-sphenoid and supra-occipital bones.

If this should prove to truly represent the general trend of evolution, especially as it affects the expansion of the parasphenoid, it might be possible to derive the Urodeles, as MOODIE has done, from the Branchiosauria, though no support to this view is afforded by Lysorophus.

For the fruitful discussion of these problems we need more facts. Much may be revealed by further study of the Devonian fishes, now being so successfully investigated by GOODRICH, WATSON, and DAY,* and we look forward with hope to a time when the internal anatomy of these forms will be as fully exposed as that of Lysorophus.

In conclusion, I should like to express my warm thanks to my friend and former pupil, Mr. LANCELOT SHARPE, B.A., for his skilful assistance in the work of building up some of the reconstructions on which this communication is based.

* GOODRICH, E. S., "Restorations of the Head of Osteolepis," 'Linn. Soc. Journ.—Zoology,' vol. 34, pp. 181–188, figs (1919); WATSON, D. M. S., and DAY, H., "Notes on some Palæozoic Fishes," 'Mem. and Proc. Manchester Lit. and Phil. Soc.,' vol. 60, No. 2, p. 52, Plates (1916).


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P.P.
Sq.
Pr.ot.
S.T.
E.O.
25.
P.P.
Sq.
Pr.ot.
Pr.At.
29.
D.
D.
H.Hy.
Pt.
G.
Qu.
Sq.
Pr.ot.
Op.ot.
E.O.
30.
D.
G.
D.
H.Hy.
Pt.
Pa.S.
G.
S.A.
Qu.
Sq.
C.
Pr.ot.
Op.ot.
33.
C.Hy.
ac.
St.
Pos.P.
E.Br.
E.Br.
E.O.
36.
D.
H.Hy.
G.
S.A.
An.
C.
C.Br.
C.Br.
C.Br.
Pa.S.
Bo.
E.o.
E.Br.
E.Br.

## EXPLANATION OF PLATE 70.

Twelve horizontal sections through the Skull of Lysorophus (specimen 2), selected from a series of 46, cut at intervals of 0·2 mm. and numbered according to their place in the series.

ABBREVIATIONS USED IN THE PLATE AND TEXT-FIGURES.

| | |
|---|---|
| *A.V.* | Anterior vacuity. |
| *A.W.* | Anterior wall. |
| *ac.* | Accessory bone. |
| *An.* | Angulare. |
| *Art.* | Articulare. |
| *B.Br.* | Basi-branchial. |
| *B.O.* | Basi-occipital. |
| *c.* | Foramen for internal carotid artery. |
| *Cl.* | Clavicle. |
| *C.Hy.* | Ceratohyal. |
| *C.Br.* | Ceratobranchial. |
| *D.* | Dentary. |
| *E.Br.* | Epibranchial. |
| *E.O.* | Exoccipital. |
| *F.pl.* | Foramen for facial nerve (palatine branch). |
| *F.xii.* | Foramen for the hypoglossal nerve. |
| *Fr.* | Frontal. |
| *G. or Gn.* | Goniale. |
| *H.Hy.* | Hypohyal. |
| *Hu.* | Humerus. |
| *m.ca.* | Metacarpal. |
| *M.V.* | Median vacuity. |
| *Mx.* | Maxilla. |
| *Na.* | Nasal. |
| *Op.ot.* | Opisthotic. |
| *P.oc.p.* | Paroccipital process. |
| *P.P.* | Posterior pillar. |
| *P.V.* | Posterior vacuity. |
| *Pa.* | Parietal. |
| *Pa.S.* | Parasphenoid. |
| *Pl.* | Palatine. |
| *Pr.mx.* | Premaxilla. |
| *Pr.At.* | Pro-atlas. |
| *Pr.Fr.* | Prefrontal. |
| *Pr.ot.* | Pro-otic. |
| *Pt.* | Pterygoid. |
| *Qu.* | Quadrate. |
| *Ra.* | Radius. |
| *S.An.* | Surangulare. |
| *S.O.* | Supra-occipital. |
| *S.T.* | Supra-temporal. |
| *Scp.* | Scapula. |
| *Sq.* | Squamosal. |
| *St.* | Stapes. |
| *Tb.* | Tabulare. |
| *Ul.* | Ulna. |
| $V_1$, $V_2$. | First and second vertebræ. |
| *Vo.* | Vomer. |

# PHILOSOPHICAL TRANSACTIONS.

## I.—*The Respiratory Exchange of Man During and After Muscular Exercise.**

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*Communicated by* Dr. J. S. HALDANE, *F.R.S.*

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(From the Physiological Laboratory, Oxford.)

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### INTRODUCTION.

A good deal of attention has been directed of late to the alteration of the respiratory exchange and respiratory quotient during muscular exercise, with a view to elucidating the character of the metabolism and the behaviour of the respiratory centre. Hitherto, it has, as a rule, been the custom to make only a few determinations of the total respiratory exchange in any one experiment at rather long intervals from one another. Such a method, though it may give the general and broader features of the respiratory exchange, especially when experiments are multiplied, is clearly ill adapted to show any rapid variations that may occur. The individual periods during which the respiratory exchange is actually determined may be too long (this length is often essential, in order to render negligible slight errors which would become significant if it were curtailed), and the long intervals between the different determinations are undesirable.

One of us, in conjunction with HALDANE, HENDERSON, and SCHNEIDER,† attempted to obtain information on the course of the total respiratory exchange in the period of rest immediately following a short and violent muscular exertion at an altitude of

* The experiments described in this paper were made in 1913, and the method we adopted, and some of our results, were described at the Nineteenth International Physiological Congress at Groningen in that year. Pressure of other work prevented us from publishing our results at that time, and during the war it was impossible for us to deal with our material, as we were on military service.

† DOUGLAS, HALDANE, YANDELL HENDERSON, and SCHNEIDER, 'Phil. Trans.,' B, vol. 203, p. 185 (1913).

 [Published, April 14, 1920.

over 14,000 feet on Pike's Peak, using for this purpose the bag method of DOUGLAS.* On this occasion, four determinations of the total respiratory exchange were made in each experiment at different intervals after the cessation of the muscular exertion, and, by making a considerable number of experiments, it was possible to obtain a fairly complete picture of the course of events in the hour-and-a-half immediately succeeding the muscular exertion. The main disadvantage was that, as the experiments had to be made on different days, the initial values for the resting respiratory exchange and respiratory quotient varied considerably in the different experiments. From a consideration of these experiments, it was, however, evident to us that the bag method could easily be adapted to give a practically continuous record of the respiratory exchange in a single experiment, and that the result would be infinitely more satisfactory than that obtained from a few observations made in each of a number of different experiments.

## EXPERIMENTAL METHOD.

The general arrangement of the apparatus used by us is shown in fig. 1. The subject sat on a Krogh bicycle ergometer,† and breathed through a mouthpiece

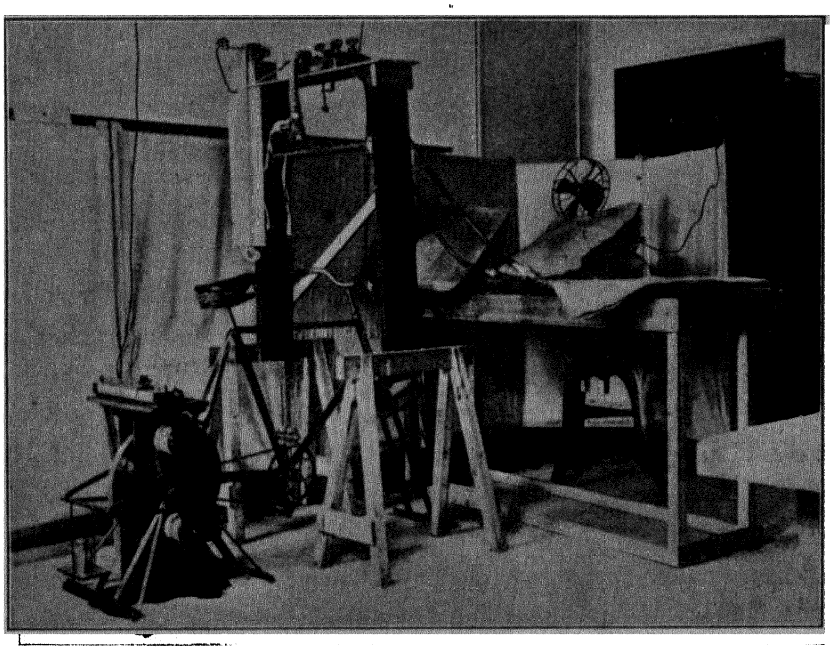


FIG. 1.

connected with inspiratory and expiratory valves. A flexible rubber pipe passed from the expiratory valve to the centre of a piece of brass tubing, into the opposite side, of which were let four short pieces of brass tubing, so that, when the ends of the pipe were included, a six-way distributing system for the expired air was formed.

* 'Journ. Physiol.,' vol. 42; Proc. Physiol. Soc.,' p. xvii (1911).

† 'Skand. Archiv f. Physiol.,' vol. 30, p. 375 (1913).

One end of the main brass tube was closed by a plain rubber stopper, the other by a rubber stopper through which passed a glass tube connected with a tambour writing on a Mackenzie polygraph. The four short pieces of brass tubing were connected to large-bore brass taps, and these in turn by means of lengths of rubber tubing to four gas bags, in which the expired air was collected, the mouth of each gas bag being fitted with a large-bore aluminium tap.* The bore of the rubber and brass tubes was $\frac{3}{4}$ inch. Fig. 2 gives a diagram of the distributing system.

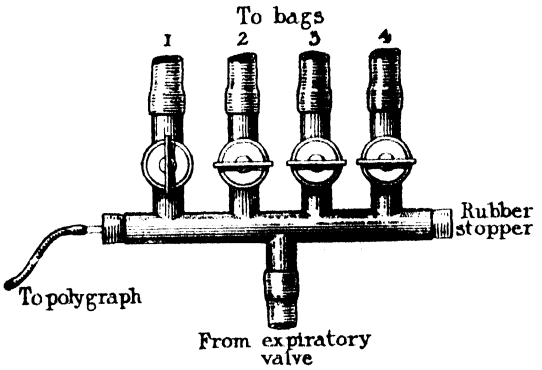



FIG. 2.

Towards the close of the investigations described in this paper, a somewhat different arrangement of the apparatus was devised, and this is shown in fig. 3. In

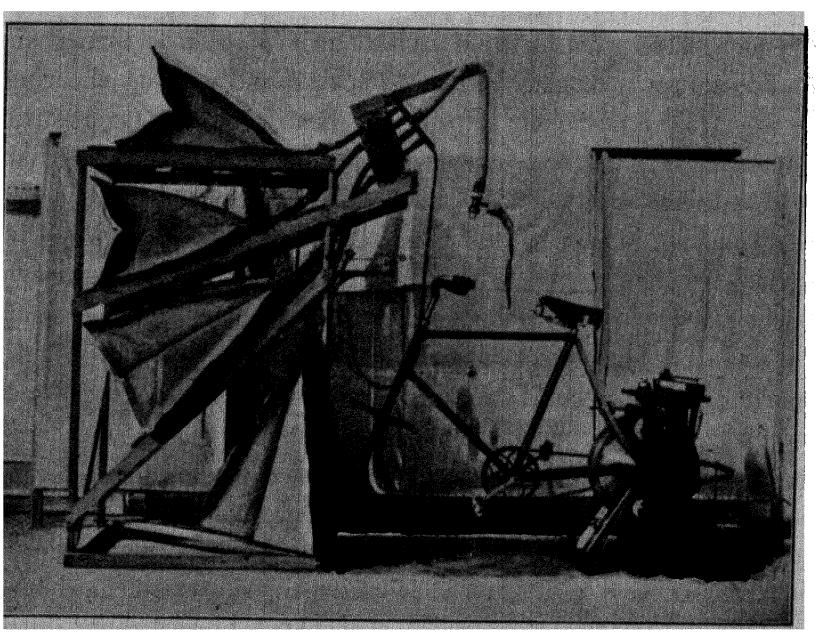


FIG. 3.

* The gas bags, aluminium taps, and valves were made by Messrs. Siebe, Gorman and Co., Westminster Bridge Road, S.E. The valves had been made of specially large bore for us, and offered hardly any appreciable resistance to the passage of even 100 litres of expired air per minute.

this form the bags were mounted one above another in a wooden framework, so that the pipes connecting the distributing system with the bags were reduced considerably in length, and the whole apparatus was rendered far more compact and convenient to work with. All the experiments described in this paper were, however, made with the arrangement shown in fig. 1.

The course of an experiment was as follows: The whole apparatus, including connecting pipes and bags, was first filled with expired air by breathing through the respiration valves. The rubber stopper was then removed from the main brass tube in the distributing system, and the bags emptied in succession by pressing on them and finally rolling them up, the taps on the distributing system being closed directly this was completed. This procedure ensured that any air remaining in the bags and connecting tubes would have approximately the same composition as the expired air entering them during the experiment, and, as the bags were always emptied through the meter in precisely the same way when measuring the volume of expired air collected, any error due to the residual volume of air in the bag was rendered negligible.

The subject then seated himself on the bicycle ergometer with his feet on the foot rests, and maintained himself in as complete a condition of rest as possible, breathing through the valves with a clip on his nose. The expired air passed through the free opening to air in the distributing system. After a preliminary period of 10 or 15 minutes, the rubber stopper was placed in the free opening at the end of an expiration, and one of the taps in the distributing system was turned simultaneously, so that the expired air was diverted into the corresponding bag, the time being noted on a stop-watch. After a sufficient sample had been collected (in about 5–6 minutes), the tap was closed at the end of an expiration and the rubber stopper simultaneously removed, the time being again noted; the subject continued to breathe through the valves to air. The bag, after turning the aluminium tap which closed its mouth, was removed from the tube connecting it with the distributing apparatus and carried to the meter (a wet meter of the Bohr pattern giving 10 litres per revolution), where the volume of expired air collected was measured, after mixing it thoroughly by frequent pressure on the bag, and a small sample was reserved for analysis. After this the empty bag was reattached to the apparatus in readiness for another sample. In some experiments, a second determination of the resting respiratory exchange was made before commencing the muscular work, the total period of rest before starting the work being correspondingly increased. The changes in pressure in the distributing system at each breath were recorded by means of the polygraph, and the tracing therefore gave the number of breaths that were taken while the expired air was being collected.

As soon as the resting respiratory exchange had been determined, the subject commenced to pedal the bicycle against the electric brake. Three different loads were employed in the different experiments, and the muscular work was kept up for

either a shorter or a longer period. The subject kept time in pedalling to a metronome placed just in front of him, set at a speed that he found to be convenient (176 revolutions of the back wheel, or 50 complete revolutions of the pedals per minute). The steadiness of the rate of pedalling was further checked by reading the automatic counter on the ergometer at intervals.

While the muscular exercise was in progress, either two or four determinations of the respiratory exchange, depending on the duration of the exercise, were made at intervals, in the same way as that described above. With the last determination of the respiratory exchange during the exercise, the collection of the samples of expired air became continuous. Directly the bag in which the last sample of expired air was collected during the exercise was full, the observer told the subject to stop working, and simultaneously closed the tap on the distributing system connected with the full bag, and opened the tap connected with one of the other bags. The moment this one was filled, he turned the expired air into the third bag, and so on, always turning the taps at the end of an expiration and noting the time on the stop-watch (we used a stop-watch with a split seconds hand, so as to allow us to note the time accurately without disturbing the continuous record of the time). As the bags were filled, they were carried away and their contents measured, reserving samples for analysis, and they were then replaced on the apparatus ready for use again. As soon as the subject received the word to stop, he replaced his feet on the foot rests and resumed his previous condition of rest, and remained thus until the close of the experiment.

In an experiment, one of us (either DOUGLAS or HOBSON) acted as subject, the second looked after the distributing taps and noted the times, while the third removed the bags as they were filled and measured their contents, noting the temperature and taking samples for subsequent analysis. Even in the experiments which involved the greatest hyperpnœa, we found that it was possible, when using four bags on the apparatus, to complete the measurement of the sample taken just before stopping the work, and to return the bag to the apparatus in plenty of time for the reception of the fourth sample after the cessation of the work. After this, the hyperpnœa had diminished to such an extent that the bags took a considerable time to fill, and measurement of the different samples became easy.

In order to keep the subject cool during the muscular exercise a current of air was allowed to play on him from an electric fan, and in the severe work experiments, two fans were used for this purpose, the fans being turned off soon after the subject ceased to work.

The general accuracy of the Douglas method for determining the respiratory exchange has been proved by CARPENTER* by comparison with different forms of the Benedict apparatus, the Zuntz-Geppert apparatus, and the Tissot apparatus. We

* "A Comparison of Methods for Determining the Respiratory Exchange of Man," 'Publication No. 216, Carnegie Institute of Washington,' 1915.

may note here that we tested the bags we employed to make sure that any diffusion of gas through the walls was negligible. CARPENTER has some distrust of the Siebe Gorman valves, but we took care to test the ones that we used in these experiments, to see whether there was any leakage backwards through the inspiration valve. For this purpose, we did two series of experiments, one at rest, the other at work. In each series determinations of the respiratory exchange were made alternately, firstly with the valves used without any safeguard, and secondly with the addition of a rubber tube 157 cm. long and 2·5 cm. in bore on to the inlet side of the inspiration valve. If there were any material leakage backwards through the valve, the expired air which had leaked out would be held up in the rubber tube, and would be rebreathed at the next breath, and the total respiratory exchange would consequently be found to be greater with the long tube than without it. The results are given in Table I.

TABLE I.

| Duration of observation. | Respiratory exchange in c.c. per minute at 0° and 760 mm. | | Respiratory quotient. | Breaths per minute. | At 37°, moist, and prevailing barometer. | |
|---|---|---|---|---|---|---|
| | $O_2$. | $CO_2$. | | | Litres breathed per minute. | C.c. per breath. |
| 5′ 47″ rest | 297 | 235 | 0·791 | 20·6 | 10·0 | 484 |
| *5 7 „ | 297 | 239 | 0·805 | 20·1 | 10·2 | 505 |
| 5 56 „ | 280 | 218 | 0·779 | 20·2 | 9·4 | 465 |
| *6 21 „ | 288 | 227 | 0·788 | 19·8 | 9 6 | 485 |
| 1 28 work | 1605 | 1538 | 0·958 | 25·2 | 41·7 | 1654 |
| *1 32 „ | 1600 | 1506 | 0·941 | 25·4 | 40·8 | 1606 |
| 2 23 „ | 1620 | 1489 | 0·919 | 25·6 | 40·5 | 1582 |
| *2 23 „ | 1668 | 1535 | 0·920 | 25·2 | 41·2 | 1635 |

* Samples taken with tube on the inspiration valve.

Rested for 10′, and worked for more than 5′ before beginning to take the samples. Work = 704 kg.m. per minute.

It will be seen that in the rest experiments there are slight differences between the successive results, but there is no definite indication that the results obtained with the addition of the long tube are higher than those without it. In the work experiments the oxygen consumption progressively increases, and the respiratory quotient falls. This, however, is quite characteristic of the respiratory exchange during work in the case of DOUGLAS, who served as the subject in these experiments (see Tables and figures below), and here again there is no distinct indication of any serious loss of the expired air by leakage backwards through the inspiratory valve. We always took care to keep the valves as vertical as possible with the inspiratory valve lowermost—an important point, as the mica discs of the Siebe Gorman valves are closed only by gravity and are not assisted by a spring.

DOUGLAS felt quite comfortable when sitting still on the bicycle, but HOBSON

always found the position rather irksome. This may account for the high respiratory exchange shown by HOBSON when at rest, for this was more than one would have expected even when one allowed for the fact that HOBSON was bigger and of greater muscular development than DOUGLAS. HOBSON was in far better muscular condition than DOUGLAS, who was quite out of training.

All our experiments were commenced about two hours after taking a light breakfast. In some respects this is an undesirable feature, but as BENEDICT and CATHCART'S experiments,* which were made on a subject in the post-absorptive state, *i.e.*, when he had taken no food for the previous 12 hours, show the same type of changes as do our experiments, we can feel tolerably certain that though the food may have influenced the degree of the changes of the respiratory exchange caused by the muscular work in our experiments, it has not seriously influenced their general character.

## EXPERIMENTAL RESULTS.

1. *Moderate Work of* 704 *kg.m. per minute.*

(*a*) Short period of muscular work, viz., about ¼ hour.

The results are given in Table II, and Experiment 4 is shown graphically in fig. 4.

These were our earliest experiments, and the data are not altogether complete, Experiments 2 and 3 lacking determinations of the respiratory exchange in the preliminary period preceding the work. During the work the respiratory exchange per minute was about 1700 c.c. of oxygen and 1500 c.c. of carbon dioxide. HOBSON showed higher values than DOUGLAS, but it may be noted that his respiratory exchange at rest was always considerably above that of DOUGLAS. After the stop of the exercise the respiratory exchange falls back extremely rapidly at first, and then more slowly to a value which, so far as can be judged from the available data, corresponds pretty closely with the preliminary resting value obtained just before the exercise commenced.

The respiratory quotient is distinctly raised during the work in Experiment 1 (DOUGLAS), and a similar rise seems probable in Experiment 3; but in Experiment 4 (HOBSON) there is little or no evidence of this rise. Both subjects are alike in showing a marked rise of the respiratory quotient to above unity in the first period following the cessation of the exercise. This rise is, however, only temporary, and the respiratory quotient shows a great diminution in the second period after the stop, and soon attains a normal level. In Experiment 4 (HOBSON), the respiratory quotient seems eventually to drop back to just the same value that it had before the exercise commenced, but in Experiments 1, 2, and 3 (DOUGLAS) there is perhaps a slight indication of a trifling drop in the respiratory quotient below the preliminary resting value and a subsequent recovery.

* BENEDICT and CATHCART, "Muscular Work," 'Publication No. 187, Carnegie Institute of Washington,' 1913.

## TABLE II.

| Successive periods of experiment. | Respiratory exchange in c.c. per minute at 0° and 760 mm. | | Respiratory quotient. | Breaths per minute. | At 37°, moist, and prevailing barometer. | | $CO_2$ per cent. in expired air. |
|---|---|---|---|---|---|---|---|
| | $O_2$. | $CO_2$. | | | Litres breathed per minute. | C.c. per breath. | |
| *Experiment* 1.—DOUGLAS. Bar. 764 mm., room temp. 15° C. Work = 704 kg.m. per minute for 14¾ minutes. No artificial cooling. | | | | | | | |
| 10′ 0″ rest | — | — | — | — | — | — | — |
| 4 42 „ | 286 | 227 | 0·793 | 15·3 | 7·6 | 499 | 3·70 |
| 12 0 work | — | — | — | — | — | — | — |
| 2 50 „ | 1665 | 1502 | 0·902 | 25·1 | 39·6 | 1578 | 4·71 |
| 2 8 rest | 788 | 855 | 1·085 | 21·6 | 25·8 | 1195 | 4·12 |
| 4 0 „ | — | — | — | — | — | — | — |
| 5 33 „ | —* | —* | 0·849 | 17·5 | —* | —* | 3·23 |
| 7 8 „ | 328 | 270 | 0·823 | 19·3 | 10·4 | 646 | 3·25 |
| 6 11 „ | 311 | 248 | 0·797 | 15·7 | 9·7 | 616 | 3·20 |
| 4 0 „ | — | — | — | — | — | — | — |
| 6 0 „ | 332 | 254 | 0·765 | — | 10·0 | — | 3·14 |
| 6 0 „ | 299 | 235 | 0·786 | — | 9·6 | — | 3·07 |
| 6 0 „ | 301 | 241 | 0·800 | — | 9·6 | — | 3·12 |
| *Experiment* 2.—DOUGLAS. Bar. 755 mm., room temp. 15·5° C. Work = 704 kg.m. per minute for 17 minutes. No artificial cooling. | | | | | | | |
| 14′ 45″ rest | — | — | — | — | — | — | — |
| 17 0 work | — | — | — | — | — | — | — |
| 2 32 rest | 728 | 772 | 1·060 | 20·1 | 24·3 | 1210 | 3·91 |
| 2 32 „ | 403 | 364 | 0·903 | 17·0 | 12·5 | 735 | 3·58 |
| 2 25 „ | 356 | 322 | 0·905 | 17·4 | 11·4 | 652 | 3·49 |
| 6 10 „ | 319 | 264 | 0·828 | 16·4 | 10·2 | 619 | 3·20 |
| 7 23 „ | 316 | 246 | 0·779 | 14·8 | 9·2 | 624 | 3·28 |
| 7 0 „ | 299 | 226 | 0·756 | 15·0 | 8·9 | 590 | 3·15 |
| 7 4 „ | 296 | 223 | 0·754 | 14·9 | 8·8 | 590 | 3·13 |
| 6 53 „ | 303 | 239 | 0·789 | 14·2 | 9·1 | 644 | 3·21 |
| 7 1 „ | 289 | 228 | 0·789 | 16·0 | 9·2 | 575 | 3·05 |
| 5 39 „ | 299 | 235 | 0·786 | 15·2 | 9·3 | 611 | 3·12 |
| *Experiment* 3.—DOUGLAS. Bar. 753 mm., room temp. 16° C. Work = 704 kg.m. per minute for 14 minutes. Cooled by one fan during work. | | | | | | | |
| 15′ 0″ rest | — | — | — | — | — | — | — |
| 12 0 work | — | — | — | — | — | — | — |
| 2 4 „ | 1652 | 1441 | 0·872 | 22·7 | 37·9 | 1670 | 4·68 |
| 2 0 rest | 752 | 818 | 1·087 | 18·0 | 24·4 | 1356 | 4·12 |
| 2 2 „ | 416 | 356 | 0·856 | 11·8 | 11·6 | 983 | 3·78 |
| 2 3 „ | 388 | 293 | 0·755 | 11·7 | 9·8 | 834 | 3·70 |
| 5 58 „ | 319 | 261 | 0·819 | 12·0 | 9·3 | 776 | 3·46 |
| 6 0 „ | 322 | 253 | 0·786 | 11·3 | 8·9 | 787 | 3·50 |
| 6 7 „ | 307 | 236 | 0·769 | 11·6 | 8·4 | 723 | 3·47 |
| 6 2 „ | 309 | 239 | 0·773 | 11·4 | 8·6 | 756 | 3·42 |
| 7 0 „ | 295 | 230 | 0·780 | 12·1 | 8·6 | 706 | 3·32 |
| 7 9 „ | 296 | 235 | 0·794 | 12·6 | 8·6 | 681 | 3·38 |
| 7 13 „ | 284 | 229 | 0·807 | 12·6 | 8·6 | 683 | 3·28 |

No lactic acid found in either the urine collected immediately before the experiment or in that collected during the experiment.

* Mistake made in measurement of expired air sample.

TABLE II—*continued.*

| Successive periods of experiment. | Respiratory exchange in c.c. per minute at 0° and 760 mm. | | Respiratory quotient. | Breaths per minute. | At 37°, moist, and prevailing barometer. | | $CO_2$ per cent. in expired air. |
|---|---|---|---|---|---|---|---|
| | $O_2$. | $CO_2$ | | | Litres breathed per minute. | C.c. per breath. | |
| *Experiment* 4.—HOBSON. Bar. 768 mm., room temp. 16·5° C. Work 704 kg.m. per minute for 15 minutes. Cooled by one fan during work. | | | | | | | |
| 5′ 0″ rest | — | | | | | | |
| 5 1 „ | 385 | 331 | 0·860 | 17·5 | 10·9 | 620 | 3·68 |
| 5 3 „ | 350 | 308 | 0·880 | 16·6 | 10·1 | 611 | 3·66 |
| 5 0 work | — | — | — | — | — | | |
| 2 33 „ | 1750 | 1571 | 0·898 | 23·9 | 36·2 | 1515 | 5·22 |
| 5 0 „ | — | — | — | — | — | | |
| 2 33 „ | 1714 | 1540 | 0·899 | 24·3 | 36·7 | 1510 | 5·05 |
| 3 3 rest | 595 | 630 | 1·059 | 20·7 | 18·8 | 909 | 4·04 |
| 2 32 „ | 354 | 322 | 0·910 | 20·5 | 11·4 | 555 | 3·42 |
| 2 28 „ | 399 | 350 | 0·877 | 19·1 | 11·7 | 613 | 3·62 |
| 7 2 „ | 370 | 332 | 0·898 | 20·5 | 11·6 | 567 | 3·45 |
| 5 30 „ | 383 | 344 | 0·898 | 19·8 | 11·5 | 583 | 3·60 |
| 7 34 „ | 314 | 304 | 0·884 | 18·6 | 10·5 | 565 | 3·50 |
| 6 3 „ | 335 | 293 | 0·875 | 18·8 | 10·4 | 554 | 3·40 |
| 8 18 „ | 341 | 301 | 0·875 | 18·4 | 10·6 | 575 | 3·41 |

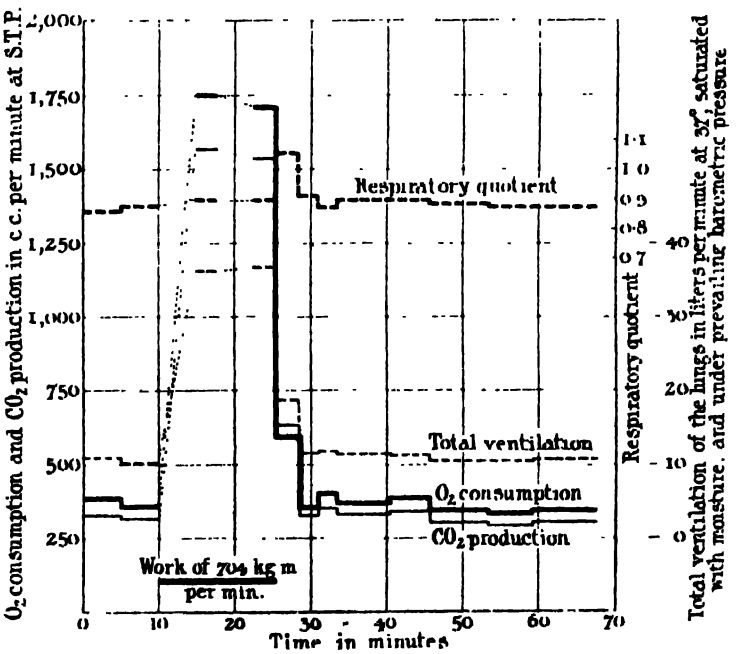



FIG. 4.

(*b*) Long period of muscular work, viz., ¾–1 hour.

The results are given in Table III, and Experiment 6 is shown graphically in fig. 5.

## TABLE III.

| Successive periods of experiment. | Respiratory exchange in c.c. per minute at 0° and 760 mm. | | Respiratory quotient. | Breaths per minute. | At 37°, moist, and prevailing barometer. | | $CO_2$ per cent. in expired air. |
|---|---|---|---|---|---|---|---|
| | $O_2$. | $CO_2$. | | | Litres breathed per minute. | C.c. per breath. | |
| *Experiment* 5.—DOUGLAS. Bar. 764 mm., room temp. 17° C. Work = 701 kg.m. per minute for 45 minutes. Cooled by one fan during work. | | | | | | | |
| 5′ 0″ rest | — | — | — | — | — | — | — |
| 5 1 „ | 294 | 239 | 0·813 | 11·6 | 8·2 | 707 | 3·53 |
| 5 0 „ | — | — | — | — | — | — | — |
| 5 1 „ | 293 | 231 | 0·788 | 10·8 | 7·8 | 724 | 3·58 |
| 5 0 work | — | — | — | — | — | — | — |
| 2 15 „ | 1611 | 1504 | 0·934 | 18·2 | 37·0 | 2030 | 4·93 |
| 10 0 „ | — | — | — | — | — | — | — |
| 2 33 „ | 1619 | 1470 | 0·908 | 20·8 | 37·3 | 1794 | 4·77 |
| 10 0 „ | — | — | — | — | — | — | — |
| 2 32 „ | 1664 | 1480 | 0·890 | 20·1 | 37·6 | 1871 | 4·76 |
| 10 0 „ | — | — | — | — | — | — | — |
| 2 34 „ | 1747 | 1504 | 0·861 | 17·5 | 37·8 | 2160 | 4·82 |
| 2 30 rest | 717 | 725 | 1·011 | 16·0 | 21·4 | 1338 | 4·10 |
| 2 30 „ | 330 | 316 | 0·957 | 11·6 | 10·5 | 905 | 3·65 |
| 2 30 „ | 302 | 262 | 0·867 | 10·0 | 8·7 | 870 | 3·65 |
| 4 0 „ | 321 | 276 | 0·860 | 10·0 | 9·3 | 933 | 3·59 |
| *Experiment* 6.—DOUGLAS. Bar. 758 mm., room temp. 15·5° C. Work = 704 kg.m. per minute for 57½ minutes. Cooled by one fan during work. | | | | | | | |
| 10′ 0″ rest | — | — | — | — | — | — | — |
| 5 0 „ | 263 | 213 | 0·808 | 9·4 | 7·1 | 754 | 3·67 |
| 5 0 work | — | — | — | — | — | — | — |
| 2 31 „ | 1624 | 1534 | 0·945 | 16·3 | 37·6 | 2310 | 4·98 |
| 22 30 „ | — | — | — | — | — | — | — |
| 2 31 „ | 1695 | 1520 | 0·897 | 17·1 | 37·8 | 2210 | 4·92 |
| 22 30 „ | — | — | — | — | — | — | — |
| 2 33 „ | 1732 | 1486 | 0·858 | 17·2 | 36·9 | 2145 | 4·92 |
| 2 31 rest | 721 | 720 | 0·998 | 13·9 | 20·8 | 1496 | 4·23 |
| 3 3 „ | —* | —* | 0·846 | — | —* | —* | 3·71 |
| 3 1 „ | 325 | 278 | 0·855 | 10·9 | 9·1 | 830 | 3·76 |
| 5 31 „ | 286 | 232 | 0·812 | 11·6 | 8·4 | 727 | 3·41 |
| 6 58 „ | 283 | 220 | 0·778 | 10·3 | 8·0 | 776 | 3·38 |
| 7 5 „ | 279 | 221 | 0·792 | 9·7 | 7·7 | 793 | 3·52 |
| 7 0 „ | 277 | 214 | 0·772 | 9·3 | 7·3 | 783 | 3·59 |
| 7 8 „ | 267 | 209 | 0·783 | 9·5 | 7·5 | 784 | 3·43 |
| 6 51 „ | 265 | 208 | 0·785 | 9·1 | 7·4 | 815 | 3·43 |
| 7 6 „ | 268 | 211 | 0·787 | 9·9 | 7·6 | 766 | 3·41 |

In one hour preceding experiment 47 c.c. urine, sp. gr. 1016. During whole experiment 265 c.c. urine, sp. gr. 1008. Lactic acid test negative in both samples.

* Mistake made in measurement of expired air sample.

TABLE III—*continued.*

| Successive periods of experiment. | Respiratory exchange in c.c. per minute at 0° and 760 mm. | | Respiratory quotient. | Breaths per minute. | At 37°, moist, and prevailing barometer. | | $CO_2$ per cent. in expired air. |
|---|---|---|---|---|---|---|---|
| | $O_2$. | $CO_2$. | | | Litres breathed per minute. | C.c. per breath. | |
| *Experiment* 7.—HOBSON. Bar. 773 mm., room temp. 15° C. Work 704 kg.m. per minute for 53 minutes. Cooled by one fan during work. | | | | | | | |
| 10′ 0″ rest | — | — | — | — | — | — | — |
| 4 43 „ | * | —* | 0·866 | 18·7 | * | —* | 3·19 |
| 5 0 work | — | — | — | — | — | — | — |
| 2 31 „ | 1664 | 1512 | 0·909 | 20·3 | 36·8 | 1814 | 4·91 |
| 15 0 „ | — | — | — | — | — | — | — |
| 2 36 „ | 1738 | 1507 | 0·867 | 21·6 | 37·8 | 1536 | 4·77 |
| 13 0 „ | — | — | — | — | — | — | — |
| 2 34 „ | 1687 | 1487 | 0·882 | 21·9 | 37·9 | 1521 | 4·69 |
| 10 0 „ | — | — | — | — | — | — | — |
| 2 33 „ | 1676 | 1481 | 0·885 | 24·7 | 37·8 | 1531 | 4·69 |
| 2 20 rest | 836 | 863 | 1·031 | 21·4 | 28·4 | 1164 | 3·64 |
| 2 19 „ | 384 | 339 | 0·883 | 19·9 | 12·8 | 642 | 3·18 |
| 2 6 „ | 396 | 311 | 0·785 | 19·5 | 11·7 | 601 | 3·18 |

* Mistake made in measurement of expired air sample.

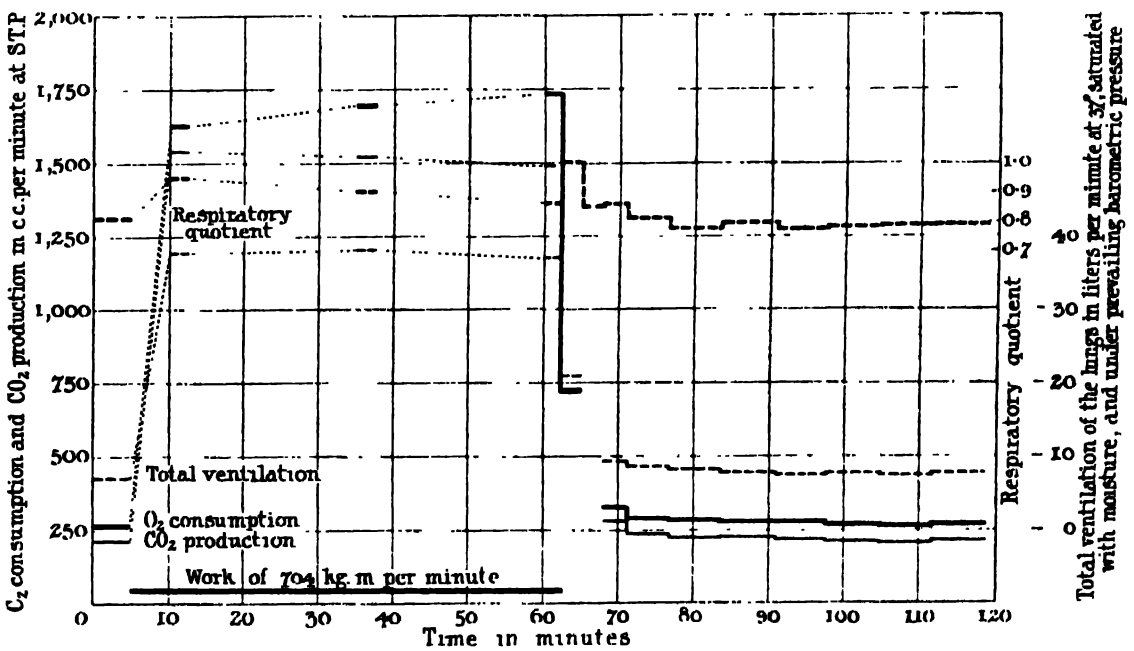



FIG. 5.

The average respiratory exchange during the exercise is practically the same as in the experiments with the shorter period of work, and there is the same rapid fall in the respiratory exchange on cessation of the exercise, and the same temporary sharp rise of the respiratory quotient immediately after the stop.

In Experiment 7 (HOBSON) the respiratory exchange remains tolerably steady throughout the whole period of work, the respiratory quotient being perhaps raised a trifle during this period, but the case is different in Experiments 5 and 6 (DOUGLAS). In these two experiments, while $CO_2$ output remains pretty constant during the whole period of exercise, or even falls slightly, the oxygen intake rises steadily throughout the work, until in the last determination made in the work period the oxygen consumption is over 100 c.c. per minute higher than in the first. The respiratory quotient which was markedly raised in the first determination during work in these two experiments on DOUGLAS, falls therefore steadily during the work period, though the final value of this quotient just before stopping the work is still very definitely above the resting value.

The respiratory exchange after the stop of the exercise was only followed for a considerable time in Experiment 6, and in this case there is apparently a slight diminution of the respiratory quotient below the initial resting value after the transitory high quotient immediately following the stop of the work has disappeared, and it is dubious whether there is any tendency to recovery of the original value during the period that the observations were kept up.

The volume of air breathed per minute in these experiments varies in a similar manner to the respiratory exchange, though the oxygen consumption shows a more rapid drop after the stop of the exercise than does either the $CO_2$ output or the hyperpnœa. During the work the total ventilation of the lungs remains pretty steady, and the increase in the ventilation of the lungs is brought about more by increasing the depth of the respirations than by increasing their rate, for the volume of each breath is increased to about thrice the initial resting value in the case of DOUGLAS (Experiments 1, 5, and 6), and the rate is less than doubled; while in the case of HOBSON (Experiment 4) these values are respectively $2\frac{1}{2}$ times and $1\frac{1}{2}$ times the resting values. An increase of depth of the breathing is, of course, a more economical method of increasing the alveolar ventilation than is an increase of rate, owing to the greater proportional influence of the dead space in shallow breathing, and one finds therefore in these experiments that though the metabolism, as judged by the oxygen consumption has about six times the resting value in the case of DOUGLAS, and $4\frac{1}{2}$ times the resting value in the case of HOBSON, the total ventilation of the lungs is only increased to five times and $3\frac{1}{2}$ times the resting values respectively.

2. *Hard Work of* 1056 *kg.m. per Minute.*

(*a*) Short period of muscular work, viz., 15 minutes.

The results of experiment on DOUGLAS are given in Table IV.

In this case the $CO_2$ production during the work remains steady, but the oxygen consumption is considerably higher in the second determination than in the first. Though the respiratory exchange falls after the stop of the exercise with a rapidity comparable with that in the previous experiments, there are some significant altera-

tions in the respiratory quotient. In the first place, there is the abnormally high respiratory quotient of unity in the first observation made in the work period, and in the second, the respiratory quotient, after the transitory sharp rise immediately after the stop of the exercise has passed away, falls to a value which is definitely below that which it had before the work was begun, and this value remains practically steady during the last four or five periods of the experiment. The respiratory exchange reaches a steady value 18 minutes after the stop of the exercise, and it will be seen that though the $CO_2$ output during the remaining 25 minutes of the experiment (a period that corresponds with the persistent low respiratory quotient), is below the value obtained during the preliminary rest period, the oxygen consumption is on the average somewhat above the initial resting value.

TABLE IV.

| Successive periods of experiment. | Respiratory exchange in c.c. per minute at 0° and 760 mm. | | Respiratory quotient. | Breaths per minute. | At 37°, moist, and prevailing barometer. | | $CO_2$ per cent. in expired air. |
|---|---|---|---|---|---|---|---|
| | $O_2$. | $CO_2$. | | | Litres breathed per minute. | C.c. per breath. | |
| *Experiment* 8.—DOUGLAS. Bar. 764 mm., room temp. 12° C. Work 1056 kg.m. per minute for 15 minutes. Cooled by two fans during work. | | | | | | | |
| 10′ 0″ rest | — | — | — | — | — | — | — |
| 5 45 „ | 281 | 233 | 0·829 | 10·4 | 8·1 | 776 | 3·50 |
| 5 0 work | — | — | — | — | — | — | — |
| 1 45 „ | 2240 | 2245 | 1·002 | 24·6 | 59·3 | 2410 | 4·58 |
| 7 0 „ | — | — | — | — | — | — | — |
| 1 34 „ | 2350 | 2250 | 0·957 | 23·3 | 59·7 | 2460 | 4·57 |
| 5 5 rest | 631 | 738 | 1·170 | 16·7 | 25·9 | 1551 | 3·45 |
| 2 58 „ | 364 | 324 | 0·891 | 14·2 | 12·4 | 874 | 3·17 |
| 5 9 „ | 350 | 301 | 0·860 | 13·4 | 11·5 | 857 | 3·18 |
| 4 46 „ | 331 | 267 | 0·806 | 12·6 | 10·1 | 803 | 3·20 |
| 5 2 „ | 291 | 229 | 0·787 | 11·7 | 9·1 | 775 | 3·07 |
| 4 47 „ | 290 | 222 | 0·765 | 10·9 | 8·6 | 789 | 3·13 |
| 5 1 „ | 275 | 211 | 0·767 | 10·2 | 8·1 | 792 | 3·17 |
| 4 52 „ | 298 | 225 | 0·755 | 12·1 | 8·9 | 731 | 3·09 |
| 5 24 „ | 283 | 225 | 0·788 | 11·1 | 9·0 | 807 | 3·02 |

In one hour preceding experiment 106 c.c. urine, sp. gr. 1011 ; lactic acid negative.
During whole experiment 245 c.c. urine, sp. gr. 1004, containing 0·10 grm. lactic acid.

It will be noted that in this case the first resting period after the stop of the exercise is much longer than in the other experiments. As a matter of fact there were two periods, but on switching the expired air from the first bag into the second the watch was by accident not stopped, though the approximate position of the hand was noted, and on this occasion it was impossible to distinguish the transition from the first to the second bag on the polygraph tracing of the respirations. In order to reckon the respiratory exchange accurately, the two periods had therefore to be taken together. The first sample took approximately 1½ minutes to collect, and

accepting this figure the respiratory exchange averaged in the first 1½ minutes after the stop of the exercise 1369 c.c. $O_2$ and 1714 c.c. $CO_2$ per minute, with R.Q. = 1·254, and in the succeeding 3′ 35″ 324 c.c. $O_2$ and 329 c.c. $CO_2$ per minute, with R.Q. = 1·016.

(*b*) Long period of muscular work, viz., 29–38 minutes.

The results are given in Table V, and Experiment 9 is shown graphically in fig. 6.

TABLE V.

| Successive periods of experiment. | Respiratory exchange in c.c. per minute at 0° and 760 mm. | | Respiratory quotient. | Breaths per minute. | At 37°, moist, and prevailing barometer. | | $CO_2$ per cent. in expired air. |
|---|---|---|---|---|---|---|---|
| | $O_2$. | $CO_2$. | | | Litres breathed per minute. | C.c. per breath. | |
| *Experiment* 9.—Douglas. Bar. 763 mm., room temp. 12° C. Work = 1056 kg.m. per minute for 37 minutes. Cooled by two fans during work. | | | | | | | |
| 10′ 0″ rest | — | — | — | | | — | — |
| 5 0 „ | 308 | 266 | 0·863 | 11·8 | 9·0 | 761 | 3·60 |
| 3 0 work | — | — | | | — | — | — |
| 1 12 „ | 2231 | 2446 | 1·095 | 25·3 | 65·6 | 2595 | 4·52 |
| 9 0 „ | — | — | — | — | — | — | — |
| 1 56 „ | 2380 | 2260 | 0·950 | 23·8 | 59·5 | 2500 | 4·61 |
| 9 0 „ | — | — | — | — | — | — | — |
| 1 45 „ | 2395 | 2270 | 0·948 | 26·0 | 63·1 | 2430 | 4·36 |
| 9 0 „ | — | — | — | — | — | — | — |
| 1 51 „ | 2420 | 2220 | 0·917 | 21·7 | 59·6 | 2415 | 4·52 |
| 2 1 rest | 1070 | 1258 | 1·175 | 30·3 | 14·5 | 1170 | 3·14 |
| 3 8 „ | 396 | 367 | 0·927 | 16·0 | 11·2 | 889 | 3·11 |
| 5 17 „ | 358 | 301 | 0·841 | 13·1 | 11·4 | 872 | 3·20 |
| 10 15 „ | 321 | 249 | 0·776 | 12·1 | 9·8 | 808 | 3·10 |
| 11 57 „ | 321 | 248 | 0·765 | 12·0 | 9·2 | 768 | 3·27 |
| 10 52 „ | 335 | 253 | 0·755 | 12·7 | 9·1 | 743 | 3·26 |
| 11 5 „ | 321 | 241 | 0·741 | 12·8 | 9·1 | 707 | 3·21 |
| 10 31 „ | 331 | 254 | 0·760 | 11·4 | 9·2 | 808 | 3·35 |
| 3 0 „ | — | — | — | — | — | — | — |
| 10 57 „ | 330 | 243 | 0·736 | 10·0 | 8·5 | 850 | 3·47 |
| In 1½ hours preceding experiment 302 c.c. urine, sp. gr. 1004; lactic acid negative. During whole experiment 193 c.c. urine, sp. gr. 1011, containing 0·05 grm. lactic acid. | | | | | | | |
| *Experiment* 10.—Hobson. Bar. 755 mm., room temp. 16° C. Work = 1056 kg.m. per minute for 28¾ minutes. Cooled by two fans during work. | | | | | | | |
| 5′ 0″ rest | — | — | — | — | — | — | — |
| 5 21 „ | 394 | 349 | 0·885 | 19·3 | 12·7 | 658 | 3·38 |
| 7 0 „ | — | — | — | — | — | — | — |
| 5 11 „ | 423 | 373 | 0·881 | 19·1 | 12·9 | 677 | 3·55 |
| 4 0 work | — | — | — | — | — | — | — |
| 1 49 „ | 2490 | 2190 | 1·000 | 25·3 | 59·0 | 2330 | 5·17 |
| 7 0 „ | — | — | — | — | — | — | — |
| 1 59 „ | 2580 | 2270 | 0·880 | 25·7 | 55·7 | 2170 | 5·00 |
| 12 0 „ | — | — | — | — | — | — | — |
| 1 52 „ | 2680 | 2325 | 0·868 | 25·7 | 54·9 | 2140 | 5·20 |
| 3 12 rest | 832 | 917 | 1·102 | 23·8 | 28·9 | 1214 | 3·90 |
| 4 15 „ | 487 | 395 | 0·811 | 21·7 | 14·6 | 624 | 3·32 |
| 4 37 „ | 464 | 405 | 0·872 | 20·6 | 14·6 | 707 | 3·42 |
| Bicycle saddle too low and subject very uncomfortable throughout the work. | | | | | | | |

TABLE V.—*continued.*

| Successive periods of experiment. | Respiratory exchange in c.c. per minute at 0° and 760 mm. | | Respiratory quotient. | Breaths per minute. | At 37°, moist, and prevailing barometer. | | $CO_2$ per cent. in expired air. |
|---|---|---|---|---|---|---|---|
| | $O_2$. | $CO_2$. | | | Litres breathed per minute. | C.c. per breath. | |
| *Experiment* 11.— HOBSON. Bar. 765 mm., room temp. 15° C. Work 1056 kg.m. per minute for 38 minutes. Cooled by two fans during work. | | | | | | | |
| 10′ 0″ rest | — | — | — | — | — | — | — |
| 6 33 „ | 375 | 323 | 0·860 | 16·9 | 11·3 | 671 | 3·45 |
| 3 6 work | — | — | — | — | — | — | — |
| 1 55 „ | 2310 | 2230 | 0·966 | 25·0 | 53·9 | 2125 | 5·01 |
| 9 10 „ | — | — | — | — | — | — | — |
| 1 50 „ | 2435 | 2250 | 0·925 | 25·1 | 56·5 | 2250 | 4·82 |
| 9 0 „ | — | — | — | — | — | — | — |
| 1 46 „ | 2400 | 2240 | 0·934 | 21·9 | 56·7 | 2280 | 4·78 |
| 9 26 „ | — | — | — | — | — | — | — |
| 1 47 „ | 2360 | 2140 | 0·907 | 24·7 | 54·2 | 2190 | 4·78 |
| 2 39 rest | 819 | 852 | 1·011 | 23·4 | 26·7 | 1141 | 3·87 |
| 3 7 „ | 426 | 389 | 0·913 | 22·8 | 14·3 | 629 | 3·29 |
| 3 22 „ | 376 | 337 | 0·896 | 22·0 | 12·8 | 582 | 3·20 |
| 7 29 „ | 395 | 331 | 0·838 | 21·4 | 12·4 | 579 | 3·24 |
| 7 53 „ | 371 | 305 | 0·822 | 20·7 | 11·7 | 567 | 3·15 |
| 8 19 „ | 355 | 293 | 0·826 | 19·7 | 11·2 | 569 | 3·17 |
| 8 46 „ | 358 | 295 | 0·824 | 20·1 | 11·1 | 550 | 3·24 |
| 7 40 „ | 334 | 269 | 0·805 | 18·9 | 10·3 | 542 | 3·18 |
| 8 10 „ | 350 | 283 | 0·809 | 19·5 | 10·6 | 541 | 3·26 |
| During the whole of the experiment and in the hour preceding it 95 c.c. urine, sp. gr. 1023, which showed only a trace of lactic acid. | | | | | | | |

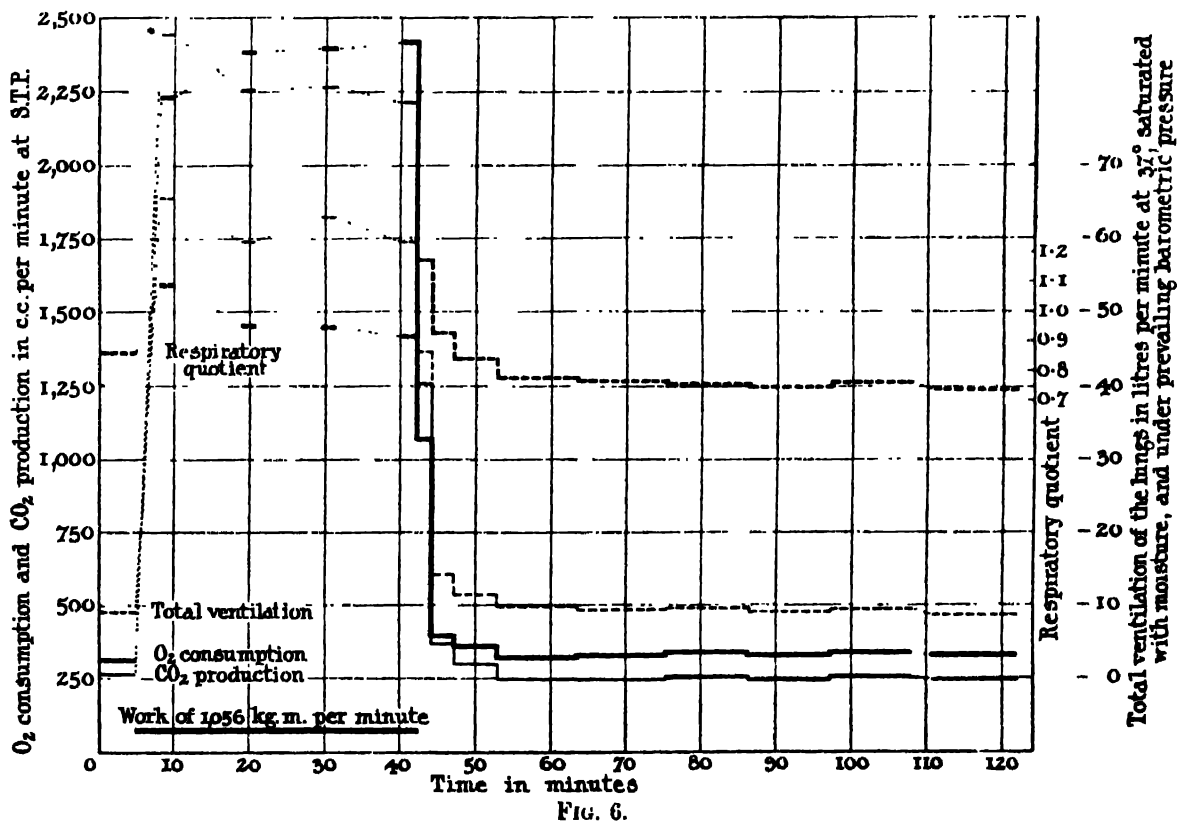



FIG. 6.

To deal first with Experiment 9 (DOUGLAS). The oxygen consumption in the first two determinations during the work period agrees closely with that found in Experiment 8. It shows a marked rise during the course of the work, and this rise is greater than was the case in Experiments 5 and 6, the oxygen consumption being 186 c.c. per minute higher in the last determination made during the work period than it was during the first. The $CO_2$ output is 112 c.c. per minute above the oxygen intake in the first work period, and the respiratory quotient well above unity at this time (it should be noted that the sample was taken at an earlier stage of the work period than in Experiment 8). The $CO_2$ output has dropped below the oxygen consumption by the time of the second observation during the work and remains fairly steady, or even diminishes slightly, during the remainder of the exercise, the respiratory quotient, which had fallen to 0·95 in the second observation, diminishing further as the oxygen consumption increases, though it is still well above the preliminary resting value in the last period of work.

After the stop of the exercise there is the usual immediate rise of the respiratory quotient followed by a rapid drop. The respiratory exchange falls rapidly, and at the end of 11 minutes has reached a value which remains practically constant for the subsequent 68½ minutes of the experiment. During this last 68½ minutes the respiratory quotient remains pretty steady at a figure considerably below the initial resting value shown at the commencement of the experiment, the diminution of the respiratory quotient being proportionally greater than in Experiment 8. The low respiratory quotient is due to the fact that the $CO_2$ output is on the average 18 c.c. per minute below the initial resting value as well as to the fact that the oxygen consumption is 20 c.c. per minute above the initial resting value. It will, moreover, be seen that the average oxygen consumption of 328 c.c. per minute during this period is considerably above what was found in the previous experiments on DOUGLAS either during the preliminary rest period or in the later stages of rest subsequent to muscular work when the respiratory exchange has reached a steady value.

To allow of comparison with Experiment 8, the first and second periods after the stop of the work may be added together. If this is done the oxygen consumption averaged 660 c.c. per minute, and the $CO_2$ output 716 c.c. per minute, with respiratory quotient 1·085, during the first 5′ 9″ after stopping the work.

In this experiment DOUGLAS was quite comfortable throughout the work, and though he felt a little tired at the end he could have continued the work for a good deal longer without serious discomfort.

Experiment 10 (HOBSON) gives a picture very similar to Experiment 9. There is the same steady rise in the oxygen consumption during the work period, the oxygen consumption being 200 c.c. per minute higher in the third determination than in the first, while the $CO_2$ output is 220 c.c. per minute lower in the second determination during the work, and 155 c.c. per minute in the third, than it was in the first. The respiratory quotient is 1·0 in the first determination during the work,

but in the second and third determinations it falls to a value identical with the initial resting figure. In this experiment HOBSON forgot to raise the bicycle saddle to the proper height, and in consequence found the work extremely uncomfortable. We were therefore compelled to terminate the work earlier than we had intended.

The experiment was therefore repeated on HOBSON some days later (Experiment 11), with the bicycle saddle at the correct height. This time he was pretty comfortable throughout the work, though he sweated a good deal notwithstanding the two fans. The picture presented in this experiment is somewhat different from that in the preceding one. The average respiratory exchange during the work is a good deal lower, as indeed one might expect since he was not subject to the disadvantage of a cramped position. Though the oxygen consumption in the three later observations during the work is higher than in the first, the rise is neither so marked as in Experiment 10 nor is it progressive. The $CO_2$ output remains constant for the greater part of the work period, but diminishes somewhat in the last determination. The respiratory quotient is only 0·966 in the first observation during the work, and shows a diminution during the course of the work, though in the last observation during the work it is still a good deal above the initial resting value. The whole course of events during the muscular work is, in fact, remarkably like that found in the case of DOUGLAS in the long experiments with lighter work (Experiments 5 and 6, Table III). Nine minutes after the work ceased, however, the respiratory quotient falls below the initial resting value, and a further fall occurs in subsequent periods, and even when the experiment terminated 48 minutes later there was no sign of recovery.

In Experiments 9 and 10 it will be seen that the hyperpnœa during the work is at a maximum in the first determination, *i.e.*, at a time corresponding to the abnormally high respiratory quotient, and $CO_2$ output, and that there is a decided drop in the amount of air breathed per minute in the subsequent observations during the exercise. This definite variation in the hyperpnœa is, however, absent in Experiment 11 in which the respiratory quotient during the work is always well below unity. If we disregard for the moment the observations which show an abnormally high respiratory quotient of 1·0 or over during the work in these experiments, since these are evidently influenced by some disturbing factor, and confine ourselves to the period during which the hyperpnœa remains fairly steady, it will be seen that in DOUGLAS'S case the oxygen consumption is increased about eight-fold during the work, while the amount of air breathed per minute is only about seven times the resting value, the rate of breathing being rather more than doubled, and the depth of the breathing rather more than trebled. HOBSON'S oxygen consumption rises during the work to rather more than six times the preliminary resting value, but the total ventilation of the lungs is barely five times the resting value, the rate of breathing being about 1½ times as great, and the depth of breathing more than three times as great, as during rest. The hyperpnœa is therefore being brought about, just as was the case

with the lighter work, more by increasing the depth than by increasing the rate of the respiration. That the hyperpnœa in the later stages of the work in these experiments is not excessive in comparison with that observed in the case of lighter work, is shown by the fact that the average volume of expired air per 1 c.c. of $CO_2$ given off is in DOUGLAS'S case, 25·2 c.c. in the experiments with work of 704 kg.m. per minute, and 26·9 c.c. in the experiments at 1056 kg.m. per minute, HOBSON giving values of 24·6 c.c. and 24·7 c.c. respectively (observations which show an abnormally high respiratory quotient being excluded as before).

3. *Severe Muscular Work of* 1232 *kg.m. per Minute.*

The results of this experiment (No. 12) are given in Table VI, and are shown graphically in fig. 7.

TABLE VI.

| Successive periods of experiment. | Respiratory exchange in c.c. per minute at 0° and 760 mm. | | Respiratory quotient. | Breaths per minute. | At 37°, moist, and prevailing barometer. | | $CO_2$ per cent. in expired air. |
|---|---|---|---|---|---|---|---|
| | $O_2$. | $CO_2$. | | | Litres breathed per minute. | C.c. per breath. | |
| *Experiment* 12.—DOUGLAS. Bar. 762 mm., room temp. 16° C. Work = 1232 kg.m. per minute for 7¾ minutes. Cooled by two fans during work. | | | | | | | |
| 21′ 27″ rest | — | — | — | — | — | — | — |
| 4 0 work | — | — | — | — | — | — | — |
| 4 0 rest | — | — | — | — | — | — | — |
| 3 0 work | — | — | — | — | — | — | — |
| 0 45 „ | 2795 | 2880 | 1·030 | 48·0 | 114·8 | 2390 | 3·06 |
| 0 51 rest | 2110 | 2390 | 1·132 | 56·5 | 105·1 | 1862 | 2·77 |
| 1 37 „ | 806 | 1011 | 1·255 | 33·4 | 44·4 | 1330 | 2·78 |
| 3 13 „ | 469 | 485 | 1·033 | 20·8 | 20·6 | 991 | 2·87 |
| 7 2 „ | 379 | 359 | 0·947 | 19·5 | 16·1 | 826 | 2·72 |
| 9 4 „ | 334 | 268 | 0·802 | 18·2 | 12·7 | 699 | 2·58 |
| 6 40 „ | 325 | 240 | 0·739 | 19·5 | 11·6 | 596 | 2·53 |
| 9 24 „ | 292 | 199 | 0·684 | 17·7 | 9·7 | 550 | 2·50 |
| 11 31 „ | 276 | 178 | 0·645 | 18·7 | 9·1 | 489 | 2·38 |
| 10 2 „ | 318 | 207 | 0·651 | 18·7 | 10·0 | 534 | 2·53 |
| 4 42 „ | — | — | — | — | — | — | — |
| 10 31 „ | 330 | 214 | 0·648 | 18·0 | 9·8 | 545 | 2·67 |
| 10 54 „ | 323 | 221 | 0·684 | 19·0 | 9·9 | 521 | 2·62 |

In one hour preceding experiment 34 c.c. urine, sp. gr. 1026; lactic acid negative.
During whole experiment 92 c.c. urine, sp. gr. 1022, containing 0·57 grm. lactic acid.

This amount of work proved too severe for the subject (DOUGLAS) to keep it up for more than a few minutes. The initial rest period lasted for 21½ minutes, but, owing to an error, we did not succeed in determining the respiratory exchange during this time. We had intended that the work should be kept up for five minutes before collecting the first sample of expired air, but, at the end of four minutes, the hyperpnœa and distress were so great that the subject could no longer tolerate

breathing into the apparatus, and he was forced to stop working. After an interval of four minutes' rest, at the end of which time the hyperpnœa had greatly diminished, though it had by no means ceased, the work was begun again. Three minutes later the respiratory exchange was determined over a period of 45 seconds, and then the subject stopped work. The after-effect of the work was followed for 85½ minutes.

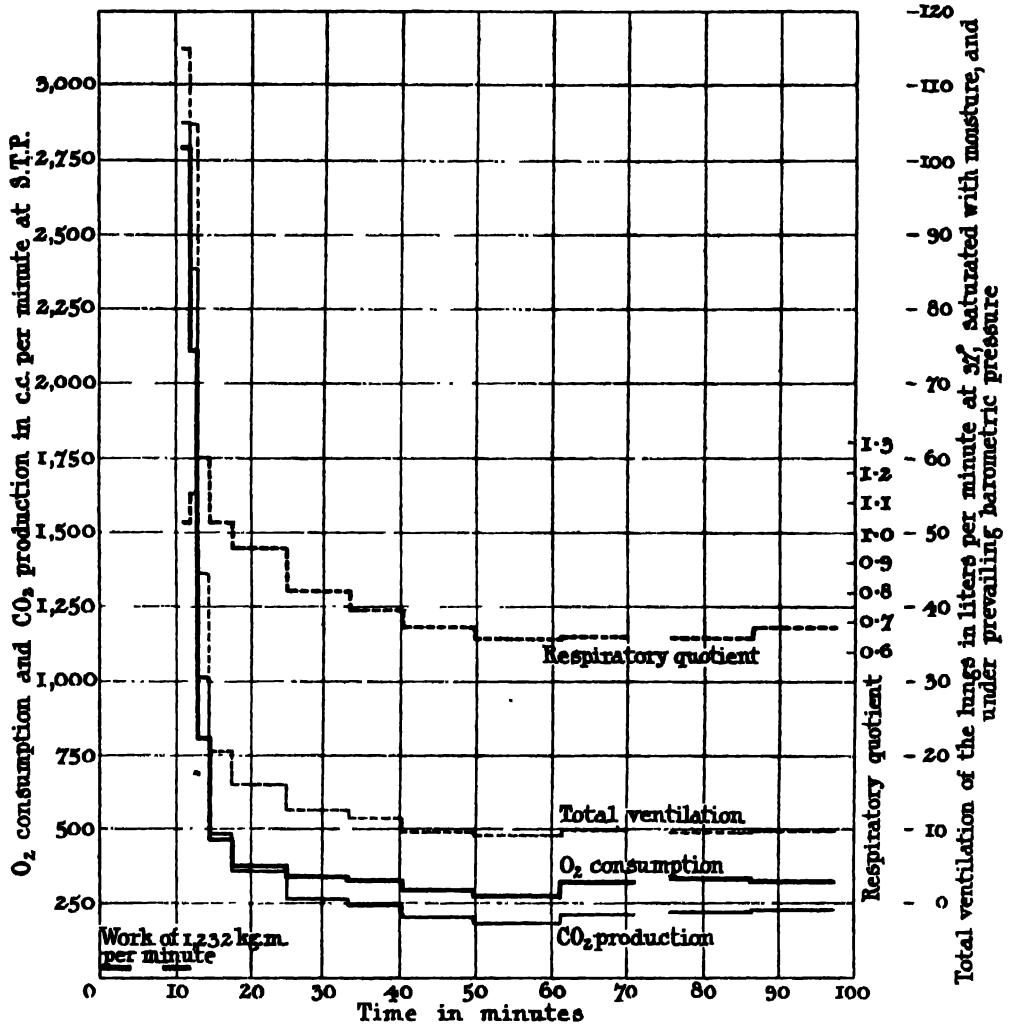



FIG. 7.

It will be seen that, in spite of the fact that the work had already lasted for a total of seven minutes, and that there had been, in addition, an interval of four minutes between the two periods of work, the $CO_2$ output is still above the oxygen consumption, and the respiratory quotient above unity, when the determination of the respiratory exchange was made just before stopping the work.

In the first minute after the stop of the work, there is only a comparatively small drop in the respiratory exchange, though there is a big diminution in the succeeding minute and a-half, and a considerable further fall in the next three minutes. The

figures show clearly how greatly the fall in the $CO_2$ output lags behind the fall in the oxygen consumption during these three periods. The respiratory exchange and respiratory quotient fall to a minimum in the eighth period after the stop (*i.e.*, between the 38th and 49th minutes), and subsequently rise again to some extent. It is possible that the lowness of the figures in the eighth period is due to some chance error, though we were unable to identify any fallacy in our measurements, and one may note that as low, or even lower, figures for oxygen consumption are recorded in Experiments 6 and 8. Taking the last 57 minutes of the experiment (seventh period after the stop of the work onwards), as a whole, the striking features are the great depression of the respiratory quotient, which lies well below 0·7, and the height of the oxygen consumption, in comparison with the lowness of the $CO_2$ output. Lower figures for $CO_2$ output in individual periods after the work are recorded during this time than in any of the other experiments on DOUGLAS, though the average $CO_2$ output for the whole period is approached in the later stages of Experiment 6.

The extreme hyperpnœa during the muscular work is obvious. Though the metabolism, as judged by the oxygen consumption, is only about ten times the average preliminary resting value, as opposed to the eight-fold increase shown in Experiments 8 and 9, the volume of air breathed per minute is practically double what it was in these experiments. What is more, this additional increase is brought about entirely by increasing the rate of the respiration, for the depth of the breathing is actually somewhat less than in Experiments 8 and 9. The excessive character of the breathing is well brought out by the extremely low percentage of $CO_2$ in the expired air (3 per cent., as opposed to 4½ per cent. or more in the previous experiments), as well as by the fact that the volume of expired air per 1 c.c. of $CO_2$ given off is 39·8 c.c., instead of the 26·9 c.c. observed in the experiments with work of 1056 kg.m. per minute; had the latter ratio held good in Experiment 12, the volume of air breathed per minute would have been only 77·5 litres instead of 114·8. The volume of air breathed per minute remains about as great during the first minute after the stop of the work as it was during the work. It then drops slowly, and attains a fairly steady value 28½ minutes after the cessation of the work. It will be noticed that the rate of the breathing during the later stages of the after-period remains much higher than in the other experiments on DOUGLAS, and that there is a corresponding reduction in the depth; a rate of 18 breaths a minute during rest has, however, often been observed in DOUGLAS under other circumstances.

## DISCUSSION OF THE RESULTS.

### (1) *The "Efficiency" during the Work.*

Though these experiments were not undertaken with the idea of determining accurately the mechanical efficiency of the body during the performance of muscular

work, *i.e.*, the relationship between the heat equivalent of the work done and the amount of heat actually liberated in the body in the performance of that work, it is of interest to calculate this value in order to compare the results with those obtained in the recent careful experiments of BENEDICT and CATHCART (*loc. cit.*), in which the muscular work was done by a trained subject in the post-absorptive state on a bicycle ergometer, and the energy output was calculated from the respiratory exchange. This may be done by using ZUNTZ and SCHUMBURG's figures* for the calorie value of oxygen at different respiratory quotients, though this method does not, of course, take into account the metabolism of protein.

In order to calculate the efficiency, one must subtract from the total heat output during the work a quantity corresponding to the "basal metabolism," on which the actual heat output corresponding to the work may be assumed to be superimposed. BENEDICT and CATHCART have discussed in detail the different values which may be selected to represent the basal metabolism. We give in Table VII the efficiency values for our experiments, using as "basal metabolism" the energy output in the preliminary rest period when sitting still on the bicycle.

TABLE VII.

| | Respiratory exchange in c.c. per minute at 0° and 760 mm. | | Respiratory quotient. | Calories produced per minute. | Extra calories per minute during work. | Calorie equivalent of work. | Efficiency. |
|---|---|---|---|---|---|---|---|
| | $O_2$. | $CO_2$. | | | | | |
| DOUGLAS. | | | | | | | per cent. |
| Preliminary rest . . | 288 | 235 | 0·816 | 1·39 | | | |
| 704 kg.m. per minute | 1668 | 1493 | 0·896 | 8·21 | 6·82 | 1·65 | 24·2 |
| 1056 „ „ | 2386 | 2250 | 0·943 | 11·91 | 10·52 | 2·17 | 23·5 |
| HOBSON. | | | | | | | |
| Preliminary rest . . | 385 | 337 | 0·873 | 1·88 | | | |
| 704 kg.m. per minute | 1705 | 1516 | 0·890 | 8·38 | 6·50 | 1·65 | 25·4 |
| 1056 „ „ | 2398 | 2210 | 0·922 | 11·87 | 9·99 | 2·47 | 24·7 |

In this Table, the respiratory exchange at rest of each subject is the average of all the values obtained on that subject before starting the work. The figures given with work of 704 kg.m. per minute are the average of all the observations made on the subject in question while this work was in progress. In the case of the work of 1056 kg.m. per minute, the figures only give the average value for the second observation during work in Experiment 8, and the last three observations during work in Experiment 9 on DOUGLAS, and the average value for the last three observations in Experiment 11 on HOBSON. Owing to the liability of the respiratory

* ZUNTZ und SCHUMBURG, 'Physiologie des Marsches,' Berlin, 1901, p. 361.

quotient to be abnormally high in the early stages with this degree of work, we must clearly discard at least the first observations during work in these experiments. We have not included Experiment 10 on HOBSON in the above Table, for it is not strictly comparable with the other experiments, because of the discomfort during the work, owing to the low position of the saddle, but this experiment shows an appreciably lower value for the efficiency than does Experiment 11, the heat equivalent of the oxygen consumption in the last two determinations during work being 12·87 calories.

In the case of DOUGLAS, previous determinations of the respiratory exchange at rest in bed immediately after waking in the morning,* have shown an oxygen consumption per minute of 237 c.c. and a $CO_2$ production of 197 c.c., with a respiratory quotient of 0·829, corresponding to a heat output of 1·15 calories per minute. Using this value for the "basal metabolism," the efficiency at 704 kg.m. per minute becomes 23·4 per cent., and at 1056 kg.m. per minute 23·0 per cent.

We made two determinations on DOUGLAS on the bicycle ergometer, when he was pedalling at the same speed as during the work, but with no load on the brake, and found an oxygen consumption per minute of 494 c.c. and a $CO_2$ production of 409 c.c., with a respiratory quotient of 0·828, corresponding to a heat production of 2·39 calories per minute. With this "basal value," which has the advantage of including the heat production involved in merely rotating the pedals, so that any extra heat production during the work corresponds more nearly simply with the output of energy entailed by putting the load on the brake, the efficiency at 704 kg.m. per minute becomes 28·4 per cent., and at 1056 kg.m. 25·9 per cent.

In whichever of these three ways the efficiency is calculated, the results are of much the same order of magnitude as those obtained by BENEDICT and CATHCART when using similar values for the "basal metabolism." If, however, the efficiency is calculated from the difference between the data obtained for each subject at the two different degrees of work, *i.e.*, for the external work of 352 kg.m. per minute, when this is superimposed on external work of 704 kg.m. per minute, the efficiency has the rather low value of 22·2 per cent. for DOUGLAS and 23·5 per cent. for HOBSON.

In those experiments in which the oxygen consumption rises progressively during the work, there is a corresponding increase in the heat production, *i.e.*, a falling off of efficiency, though the fall of efficiency is not quite proportional to the rise of oxygen consumption owing to the alteration of the respiratory quotient. For instance, in Experiment 6 on DOUGLAS, the heat production per minute during the work is 8·10 calories at the first observation, 8·35 at the second, and 8·45 at the third, and there is the same type of alteration in Experiment 5. This effect suggests the influence of fatigue, the more so, as HOBSON, who was in better muscular condition than DOUGLAS, only showed this phenomenon in Experiment 10, in which he was considerably hampered by the low position of the bicycle saddle, and had in

* DOUGLAS, HALDANE, HENDERSON, and SCHNEIDER, *loc. cit.*

consequence an exceptionally high rate of metabolism. A similar slight rise of heat production during the course of muscular work is shown in a few of BENEDICT and CATHCART'S experiments, but it is noticeably absent in the majority, especially in an experiment in which a trained cyclist rode the bicycle ergometer continuously for a period of 4 hours and 22 minutes, during the whole of which time his oxygen consumption per minute was close on 2000 c.c. One may note, too, that the heat production was practically constant in Experiment 9 on DOUGLAS in the last three observations during the work, a period of 23½ minutes, though the oxygen consumption rose considerably between the first and second observations. ZUNTZ and SCHUMBURG* have found a decreased efficiency during walking, as the result of a long march, which they ascribe to the effects of fatigue, but BENEDICT and MURSCHHAUSER† have not been able to find definite evidence of this, though the distance walked reached as much as 14 miles; the pace, however, in their longest experiments was only about 3 miles per hour.

### (2) *The Respiratory Exchange during the Work.*

We made no attempt to determine the respiratory exchange during the very early stages of the work, though it would naturally have been of great interest to follow the transition from rest to work as well as from work to rest. We felt, however, that as it takes a brief time for the subject to pick up the rate of the metronome and to steady down to the work, the results would be somewhat difficult to compare with those obtained at a later stage, and we preferred therefore to allow from three to five minutes to elapse after starting pedalling before we took our first samples, so as to allow the subject to get into reasonable equilibrium with the work.

(i) *Work of 704 kg.m. per minute.*

While DOUGLAS invariably shows a definite rise of the respiratory quotient throughout the period of work, HOBSON'S respiratory quotient remains practically steady at the same level as in the preliminary resting period. DOUGLAS'S respiratory quotient is highest in the earliest period of work, and diminishes slowly and steadily as the work is continued, though it is considerably above the preliminary resting value even when the work has been kept up continuously for ¾–1 hour.

Such a rise of the respiratory quotient might be determined by one or more of several causes. Thus it might be an indication of a real alteration in the character of the metabolism, and imply that during work a greater proportion of the necessary energy is derived from carbohydrate than during rest. On the other hand, the explanation might be found in some cause which leads to an expulsion of $CO_2$ from the store held in combination in the body (the so-called "preformed" $CO_2$) without

* *Loc. cit.*, p. 259.

† BENEDICT and MURSCHHAUSER, "Energy Transformations during Horizontal Walking," 'Publication No. 231, Carnegie Institute of Washington,' 1915.

any corresponding variation in oxygen consumption, or necessary alteration in the character of the metabolic processes in the tissues.

Two factors at least which might be responsible for the latter effect suggest themselves at once, namely, (*a*) shortage of oxygen arising from the increased oxygen requirements of the body, and (*b*) general rise of body temperature due to the muscular exertion.

In recent years the phenomena of deficiency of oxygen which may arise during muscular work have been ascribed, at least during severe exertion, to the action of lactic acid liberated in the active muscles in consequence of the metabolism of these muscles out-running the available oxygen supply that can be furnished by the blood stream,* and RYFFEL has, in fact, shown the presence of lactic acid in blood and urine as a result of hard muscular work.†

Lactic acid arising in this way will give rise to several effects. It will lower the alkalinity of the blood, and, since the activity of the respiratory centre is dependent on the hydrogen ion concentration in the blood, thus aid carbonic acid to excite the respiratory centre, a lower partial pressure of $CO_2$ being required to stimulate the centre to a given degree than would be the case in the absence of lactic acid. As lactic acid which has reached the blood stream is extremely slowly eliminated or destroyed (see Ryffel's data), it will tend to accumulate, and the hyperpnœa will, consequently, become much greater than one would expect from the $CO_2$ stimulus alone. If the excessive hyperpnœa caused in this way is sufficiently great, the alveolar $CO_2$ pressure may actually be reduced below the normal resting threshold value, in spite of the greatly increased production of $CO_2$ due to the muscular work, and directly this happens preformed $CO_2$ must be washed out of the body, the expulsion of this preformed $CO_2$ being unaccompanied by any corresponding increase in the oxygen absorption.

What is more, lowering of the alkalinity of the blood in severe muscular work is associated with a decrease in the absorption power of blood for $CO_2$,‡ and this decrease may be enormous with very severe work. A sudden diminution in the absorption power of blood for $CO_2$ must be accompanied by a great rise in the partial pressure of $CO_2$ in the blood, with, of course, an increase of the hydrogen ion concentration in correspondence, and consequently, if the muscular work is sufficiently severe to lead to the formation of lactic acid, the hyperpnœa must be still more exaggerated at the start until the redundant preformed $CO_2$ can be eliminated.

Were lactic acid to continue to accumulate, there is little doubt that the subject would find the work too severe for him, and he would soon be forced to stop; but

* DOUGLAS and HALDANE, 'Journ. Physiol.,' vol. 38, p. 420 (1909). See also DOUGLAS, HALDANE, HENDERSON, and SCHNEIDER, *loc. cit.*; and DOUGLAS, 'Ergebnisse der Physiol.,' 1914. p. 391.

† RYFFEL, 'Journ. Physiol.,' vol. 39, p. xxix, Proc. (1910).

‡ CHRISTIANSEN, DOUGLAS, and HALDANE, 'Journ. Physiol.,' vol. 48, p. 244 (1914); MORAWITZ and WALKER, 'Biochem. Zschr.,' vol. 60, p. 395 (1914).

there is some evidence to suggest that if lactic acid production is not very great and the work can be kept up for a considerable time, the rate of production of lactic acid will presently be balanced by the rate of its elimination or destruction, and a condition of equilibrium will be reached in which the threshold stimulating value of $CO_2$ on the respiratory centre will remain constant at some point which is below the normal and dependent on the steady amount of lactic acid present, and the ventilation of the lungs will now be determined, in the absence of other disturbing factors, by the height of the $CO_2$ pressure in the arterial blood above the new threshold stimulating value, not above the normal threshold value.

So long as expulsion of preformed $CO_2$ is occurring without corresponding increase in the absorption of oxygen, the respiratory quotient must be abnormally high, and muscular work of sufficient severity to give rise to lactic acid will therefore be characterisd both by excessive hyperpnœa and output of $CO_2$ and by an abnormal rise in the respiratory quotient. These changes will presumably be most marked at the commencement of the muscular exertion when the body is, so to speak, suddenly flooded with lactic acid, and there has not yet been time for any material reduction in the amount of preformed $CO_2$ in the body. Should, however, a balance be struck between production of lactic acid and its elimination, the abnormal hyperpnœa and respiratory quotient of the early stages will gradually diminish as the excess of preformed $CO_2$ is got rid of, till finally a condition of equilibrium will be reached in which the ventilation of the lungs will again become proportional to the mass of $CO_2$ given off, just as is the case in the absence of lactic acid or other disturbing factors, and the respiratory quotient will once more afford a true index of the character of the metabolism in the tissues. At this stage, even though the initial hyperpnœa has shut down to some extent, it of course remains in excess of what one would expect from the $CO_2$ stimulus alone, since there is also the constant action of lactic acid to be reckoned with.

If lactic acid is still present when the muscular work stops, the lowering of the threshold exciting value of $CO_2$ on the respiratory centre will become evident as the hyperpnœa dies away, since a considerable time elapses before the excess of lactic acid disappears, and a minute or two after the stop, the resting alveolar $CO_2$ pressure falls below the normal value. As the lactic acid disappears, a quantity of $CO_2$ must be retained to make up for the amount of preformed $CO_2$ originally expelled, and this will be accompanied by a gradual rise in the threshold stimulating value of $CO_2$ on the respiratory centre (*i.e.*, on the resting alveolar $CO_2$ pressure), as was shown by DOUGLAS and HALDANE, the normal threshold value being regained when the whole of the lactic acid has been eliminated. While $CO_2$ retention is occurring in this way, the respiratory quotient will be abnormally low, since there will be no corresponding reduction in oxygen consumption. If lactic acid production is limited only to the early period of the work, we should expect to find evidence of this

compensatory $CO_2$ retention at a later stage of the work, and possibly no indication of the presence of lactic acid when the work stops.

Lactic acid has so far only been definitely recognised in severe muscular work. It is, however, possible to imagine another method by which want of oxygen might exert its effect, and this might come into play with milder degrees of work. Thus supposing the arterial blood is not quite fully saturated with oxygen during the work, owing to the rate of passage of oxygen through the pulmonary epithelium being insufficient, and that this slight depression of the arterial oxygen pressure is in itself capable of exerting an effect on the respiratory centre, the threshold stimulating value of $CO_2$ on the respiratory centre will be lowered. Such an effect of want of oxygen will, however, presumably remain constant when the body has settled down to the work and be limited to the time during which the muscular work is actually in progress, for it should vanish with the reduction in the oxygen consumption on the cessation of the work. If this effect is sufficiently great to cause the alveolar $CO_2$ pressure to fall below the normal threshold value during the work, it should lead to temporary exaggerated hyperpnœa and expulsion of preformed $CO_2$ with an abnormally high respiratory quotient, just as does the accumulation of lactic acid. In this case, however, one would expect that apnœa would ensue when the oxygen want is relieved on the stop of the work and compensatory retention of $CO_2$ is taking place, for the threshold stimulating pressure of $CO_2$ on the respiratory centre should at once return to its old normal value, unless of course the deficiency of oxygen has led (in the absence of lactic acid) to some more lasting alteration of the threshold $CO_2$ pressure by a change in the "fixed alkalinity" of the blood, a condition which appears to come into force during prolonged exposure to atmospheres in which the oxygen pressure is reduced, *e.g.*, at high altitudes.

With a less degree of oxygen want of this type the effect should be of a different character All that will happen will be that throughout the work the hyperpnœa will be somewhat greater, and the alveolar $CO_2$ pressure somewhat lower than would be expected if $CO_2$ alone afforded the stimulus to the respiratory centre; yet here again the correlation of the activity of the respiratory centre with the varying metabolism of the tissues will depend on $CO_2$, since the want of oxygen may be regarded merely as exerting a constant action during the work and causing the respiratory centre to respond to a greater degree than normal for a given rise of $CO_2$ pressure. So long as the alveolar $CO_2$ pressure during the work does not fall below the normal threshold value there will be no expulsion of preformed $CO_2$. Consequently, a determination of the total respiratory exchange ought under these circumstances to afford evidence neither of excessive output of $CO_2$ nor of temporary great exaggeration of the hyperpnœa, while the respiratory quotient should continue to afford a true indication of the character of the metabolism of the tissues. The effect of such a want of oxygen will only be rendered apparent during the work by studying the relationship of the hyperpnœa to the alveolar $CO_2$ pressure at the time.

A "direct" effect of want of oxygen on the respiratory centre of this nature might of course be superimposed on the effects due to accumulating lactic acid in the case of severe work.

In DOUGLAS'S case the behaviour of the $CO_2$ output and of the hyperpnœa do not appear to conform with what is required by the "lactic acid" or gross want of oxygen theories as stated above, for these values remain practically constant throughout the whole period of work, in spite of the slow steady rise in the oxygen consumption and corresponding fall in the respiratory quotient. No support is therefore given to the lactic acid hypothesis in this case.

In Experiments 3 and 6 we analysed the urine passed just before the experiment began, and that passed just after it terminated, for lactic acid by RYFFEL'S method,* and found in the second sample no more lactic acid than the trace found in the first. Our determinations of lactic acid were not made with the greatest care in these experiments, and the results given in Tables II–VI should be regarded as approximate: the trace of lactic acid found in the normal resting urine is referred to as negative in these Tables.

The actual identification of lactic acid in the urine is, however, probably too coarse a method to adopt if the production of lactic acid is small, for lactic acid might get destroyed in whole or part before it could be excreted by the kidneys, and RYFFEL shows in fact that after severe exercise, excess of lactic acid in the urine disappears more rapidly than does that in the blood.

Far the most delicate test for the lowering of the alkalinity of the blood owing to deficiency of oxygen or production of lactic acid is to be found in the reaction of the respiratory centre. DOUGLAS and HALDANE (*loc. cit.*) showed that if the alveolar $CO_2$ pressure is determined at intervals whilst resting after the stop of some severe muscular work, it shows a characteristic fall to a value much below normal, followed by a slow recovery, indicating that the threshold stimulating value of $CO_2$ on the respiratory centre has been temporarily lowered by the exercise. This reaction is, however, absent after gentle or moderate exercise, the threshold value after the exercise being the same as it was before.

We made three experiments on DOUGLAS by this method, using the HALDANE-PRIESTLEY method of obtaining alveolar air samples and employing the same degree of work as in the determinations of the respiratory exchange. The results are given in Table VIII.

The figures show that there was a definite, though small, temporary lowering of the alveolar $CO_2$ pressure after the exercise in the first only of these experiments, but it should be noted that the subject was not cooled by the fan in this experiment.

It is known that rise of body temperature in an otherwise normal person is associated with a degree of hyperpnœa out of proportion to the $CO_2$ production at

* 'Journ. Physiol.,' vol. 39, p. v, Proc. (1909).

TABLE VIII.

| | Percentage of $CO_2$ in dry alveolar air. | Pressure of $CO_2$ in mm. Hg in alveolar air at 37° saturated with moisture. | Rectal temperature, degrees Fahrenheit. |
|---|---|---|---|
| (1) Work of 704 kg.m. per minute for 12 minutes. | | No cooling by fan. | Bar. 765 mm. |
| Normal before start | 5·58 | 40·0 | |
| 3½′ after stop | 5·25 | 37·7 | |
| 12 ,, | 5·29 | 38·0 | |
| 25½ ,, | 5·23 | 37·6 | |
| 45 ,, | 5·52 | 39·6 | |
| 63½ ,, | 5·46 | 39·2 | |
| (2) Work of 704 kg.m. per minute for 21 minutes. Bar. 764 mm. | | Cooled by one fan during work. | |
| Normal before start | 5·29 | 38·0 | 99·6 |
| 3½′ after stop | 5·31 | 38·1 | |
| 11 ,, | 5·14 | 36·9 | |
| 15 ,, | — | — | 99·8 |
| 23½ ,, | 5·39 | 38·7 | |
| 37 ,, | 5·31 | 38·1 | |
| 52 ,, | 5·32 | 38·2 | |
| (3) Work of 704 kg.m. per minute for 20½ minutes. Bar. 742 mm. | | Cooled by one fan during work. | |
| Normal before start | 5·61 | 39·0 | 98·8 |
| 3½′ after stop | 5·74 | 39·9 | |
| 10½ ,, | 5·68 | 39·5 | |
| 17 ,, | — | — | 99·8 |
| 22 ,, | 5·47 | 38·0 | |
| 34 ,, | — | — | 99·2 |
| 37 ,, | 5·58 | 38·8 | |

the time.* As HALDANE pointed out to us, the temperature which really matters in this connection is that of the blood reaching the respiratory centre. This, unfortunately, is practically impossible to estimate, since the blood coming from parts of the body which are abnormally warm owing to heightened metabolism is mixed in the heart with cooled blood coming from the skin. It is clear that a temporary rise in temperature of the blood reaching the respiratory centre during muscular work might give rise to alterations in the hyperpnœa, $CO_2$ output and respiratory quotient of the same sense as those caused by the development and disappearance of lactic acid. We recognised the difficulties of the question of temperature, but the best we could do was to try by means of fans to keep the general body temperature within reasonable limits during the work, for we were afraid that it might otherwise rise unduly in the still air of the laboratory. One fan was sufficient to keep the subject cool and comfortable in experiments at work of 704 kg.m. per minute, though two were necessary in

* HALDANE, 'Journ. of Hygiene,' vol. 5, p. 503 (1905); HILL and FLACK, 'Journ. Physiol.,' vol. 38, p. lvii, Proc. (1907).

the experiments with harder work. In each case the sweat evaporated almost as fast as it was formed, and the subject did not therefore get chilled in the long period of rest that followed the muscular exertion. From the data given in Table VIII, where a few determinations of the rectal temperature before and after the muscular work are recorded, we should judge that our efforts to prevent undue rise of temperature had been tolerably successful, though it is quite possible that in the first of these experiments the distinct fall in the alveolar $CO_2$ pressure after the work is dependent more on rise of temperature than on anything else, as no fan was used.

The lactic acid theory and temperature changes therefore appear inadequate to explain the rise of the respiratory quotient during the work in DOUGLAS'S case in this series of experiments, and, as we have pointed out above, a slight "direct" action of deficiency of oxygen on the respiratory centre, if limited to the period of work, would not be appreciable in a record of the total respiratory exchange, though it might become evident from a consideration of the volume of air breathed during the work and the prevailing alveolar $CO_2$ pressure. We suggest, therefore, that this alteration is, in the main at least, due to the fact that the energy output during the work involves the metabolism of a greater proportion of carbohydrate to fat than is the case during rest.

This idea is strengthened by the earlier experiments on DOUGLAS during walking exercise,* in which it was shown that rise of respiratory quotient could be detected at rates of exercise so low as to demand only double the resting metabolism, though the rise became greater as the rate of walking and the total metabolism increased, and that moderate prolongation of the exercise did not lead to any striking alteration of the respiratory quotient. It was tentatively suggested on these grounds, as well as on the fact that examination of the alveolar air gave no indication of a persistent lowered threshold value of $CO_2$ unless the pace of walking was very fast, that the most probable explanation lay in the increased proportion of carbohydrate to fat consumed during the work. AMAR,† using a bicycle ergometer, had previously obtained very similar results and had reached the same conclusion. A number of BENEDICT and CATHCART'S experiments show a fairly considerable rise of respiratory quotient during the work, with in some cases a tendency to diminution with prolongation of the exercise, though in a good many instances the respiratory quotient remains just about the same during the work as it was during the preliminary resting period, as was the case with HOBSON in our experiments. The average of their experiments shows that there is a distinct, though slight, rise of respiratory quotient during the work, and in a full discussion of the significance of this change they incline strongly to the view that it indicates an increase in the proportion of carbohydrate consumed. BENEDICT and MURSCHHAUSER'S experiments on trained athletes during walking exercise afford many examples of a rise of respiratory quotient during the exercise, and

* DOUGLAS, HALDANE, HENDERSON, and SCHNEIDER, *loc. cit.*

† AMAR, 'Le Rendement de la Machine Humaine,' Paris, 1910.

though this change is most marked when the subject had had food shortly before the commencement of the experiment, it also occurs to a less degree when he was in the post-absorptive state. The diminution of respiratory quotient during long periods of exercise is also shown in these experiments. Apparently, therefore, our experiments are not vitiated by the fact that the subjects had had breakfast about two hours before the commencement, though no doubt the degree of alteration that we observed was exaggerated by the fact that the subjects were not in the post-absorptive state.

If the view is right that carbohydrate may be used in greater proportion during work than during rest, a diminution of respiratory quotient during the work would seem by no means improbable, since the degree of rise will no doubt be to some extent dependent on the availability of carbohydrate, and this will quite likely be lessened as the stores of carbohydrate in the muscles or in the body at large are depleted in consequence of the heightened metabolism. It is clear from all these experiments that there is a good deal of difference between different individuals, and between the same individual at different times, as regards the character of their metabolism. Some, like HOBSON, seem to have much the same type of metabolism during work as during rest, at least under circumstances when the work is not very hard, while others like DOUGLAS appear to consume an increased proportion of carbohydrate, as indicated by a definite rise of respiratory quotient, even when the work is quite light. It is, of course, possible that the degree of physical fitness for the work in question may be of importance in this connection.

It is of interest to consider whether it is possible in these experiments to explain the hyperpnœa merely by a rise of $CO_2$ pressure in the arterial blood along the lines originally suggested by HALDANE and PRIESTLEY.* KROGH and LINDHARD† have raised a valid objection to direct determinations by the HALDANE–PRIESTLEY method of the alveolar $CO_2$ pressure (with which the arterial blood must be nearly in equilibrium) during muscular work, and one must therefore use an indirect method, though the direct method is applicable during rest.

The average normal alveolar $CO_2$ percentage during rest was about 5·5 per cent. in DOUGLAS (Tables VIII and IX). Taking an average of all the observations during the period of rest before commencing the work (Tables II to VI), the volume of each breath was 703 c.c. and the $CO_2$ percentage in the expired air 3·6 per cent. Calculation from these figures gives an effective dead space at rest of 244 c.c. (this includes the dead space of 60 c.c. in the valves and mouthpiece). An average of all the observations on DOUGLAS during work of 704 kg.m. per minute shows a volume for each breath of 1974 c.c. and an expired $CO_2$ percentage of 4·83 per cent. If we assume that the dead space during the hyperpnœa caused by the work has the same value as during rest, the calculated alveolar $CO_2$ percentage during the work is

* HALDANE and PRIESTLEY, 'Journ. Physiol.,' vol. 32, p. 225 (1905).

† KROGH and LINDHARD, 'Journ. Physiol.,' vol. 47, p. 30 (1913); *ibid.*, p. 431.

5·51 per cent., *i.e.*, a value identical with the resting normal. Any increase in the dead space during the work above the normal resting value would, of course, imply an increase in the alveolar $CO_2$ percentage.

We have previously shown* that the effective dead space shows a considerable increase during the hyperpnœa, caused by breathing air containing $CO_2$ when the oxygen consumption and $CO_2$ production are practically the same as during rest, and HALDANE† and YANDELL HENDERSON, CHILLINGWORTH and WHITNEY,‡ have shown that the effective dead space increases rapidly with the depth of the breaths in experiments in which the depth of the breathing was altered voluntarily. KROGH and LINDHARD,§ on the contrary, maintain that the effective dead space is hardly altered at all, no matter whether the breathing is deep or shallow. While it seems to us possible that the method of investigation adopted by KROGH and LINDHARD may give information regarding the volume of air contained in the respiratory passages, including trachea, bronchi and bronchioles, and its variations, we are not convinced by their argument that this anatomical dead space is identical with the true effective dead space, which is a purely conventional though very convenient expression, by which we assume the expired air to be composed of a mixture of average "alveolar air" with pure air contained in the "dead space."

Our previous experiments on DOUGLAS have shown that, during a hyperpnœa, caused by breathing air containing $CO_2$, a rise of 0·28 per cent. in the alveolar $CO_2$ percentage at normal barometric pressure (*i.e.*, of 2 mm. pressure of $CO_2$) is sufficient to cause a rise of 10 litres in the total ventilation of the lungs. If we suppose in our present experiments that, during work of 704 kg.m. per minute, the threshold stimulating value of $CO_2$ on the respiratory centre remained the same as during rest, corresponding to 5·5 per cent. of $CO_2$ in the alveolar air, the average rise during the hyperpnœa of about 30 litres above the normal total ventilation of the lungs at rest would have required a rise of about 0·84 per cent. above the resting alveolar $CO_2$ percentage to account for it. With the average volume of each breath at 1974 c.c., and expired $CO_2$ percentage of 4·83 per cent., the required percentage of $CO_2$ in the alveolar air (viz., 6·34 per cent.) would have been obtained if the effective dead space (including valves) had been 472 c.c. So far as we can judge from the experiments by ourselves, by HALDANE, and by HENDERSON and his colleagues, this value for the dead space is quite reasonable, having regard to the depth of the breathing. At the same time, it should be remembered that the rise of alveolar $CO_2$ pressure, that we should otherwise expect to find to account for the hyperpnœa, would be proportionally lowered if there were any "direct" action of slight deficiency of oxygen on the respiratory centre during the period of muscular work.

* CAMPBELL, DOUGLAS, and HOBSON, 'Journ. Physiol.,' vol. 48, p. 303 (1914).

† 'Amer. Journ. Physiol.,' vol. 38, p. 20 (1915).

‡ 'Amer. Journ. Physiol.,' vol. 38, p. 1 (1915).

§ 'Journ Physiol.,' vol. 51, p. 59 (1917).

In the case of HOBSON, we have only two earlier determinations of the normal alveolar $CO_2$ percentage at rest,* and these give an average value of 5·2 per cent. If we accept this value, his resting dead space in our experiments was about 205 c.c., and, if this had remained unchanged during the muscular work, his alveolar $CO_2$ percentage during the work would have been about 5·6 per cent., *i.e.*, above the resting value.

(ii) *Work of* 1056 *kg.m. per Minute.*

Experiments 8 and 9 on DOUGLAS, and Experiment 10 on HOBSON, show a quite abnormal rise of the respiratory quotient to unity or beyond in the early period of the work. This large rise is, however, quite shortlived, for, by the time the second observation is made, the respiratory quotient has fallen to about 0·95 in DOUGLAS'S case and to 0·88 in HOBSON'S. After the temporary sharp rise of the respiratory quotient has passed away, the picture presented for the remainder of the period of muscular work is very similar to that shown in the experiments at 704 kg.m. per minute, *i.e.*, DOUGLAS'S respiratory quotient remains at a level considerably above the resting value, with a tendency to fall as the work is prolonged and the oxygen consumption rises, while HOBSON'S returns to about its preliminary resting value. It will be noted in Experiments 9 and 10 that the $CO_2$ output during the first work period is markedly in excess of what it is subsequently, and that the hyperpnœa is definitely at a maximum during the same period. In the later work periods, both $CO_2$ output and hyperpnœa have dropped back to fairly steady values.

These changes shown in the early period of the exercise can be explained quite simply on the "lactic acid" hypothesis, coupled, it may be, with a more direct action of want of oxygen on the respiratory centre, for there is clear evidence of excessive hyperpnœa and washing out of pre-formed $CO_2$ at this time. Moreover, 0·1 grm. of lactic acid was recovered from the urine passed at the end of Experiment 8, and 0·05 grm. at the end of Experiment 9.

In addition to this, we obtained definite evidence in DOUGLAS' case of a persistent, though not very great, lowering of the threshold stimulating value of $CO_2$ on the respiratory centre by following the alveolar air changes after the cessation of work at 1056 kg.m. per minute. The figures are given in Table IX.

It will be seen that the resting alveolar $CO_2$ percentage fell from the normal of about 5·5 per cent. to about 5·1 per cent. between roughly the fourth and twentieth minutes after the stop (*i.e.*, a fall of about 2½ mm. below the normal alveolar $CO_2$ pressure). The general rise of body temperature seems in this instance again to have been fairly effectively controlled by the arrangements we adopted for cooling the subject.

The shortness of the period during which the abnormally high respiratory quotient and excessive hyperpnœa are shown in these experiments, and the slightness of the

* CAMPBELL, DOUGLAS, HALDANE, and HOBSON, 'Journ. Physiol.,' vol. 46, p. 301 (1913).

TABLE IX.

| | Percentage of $CO_2$ in dry alveolar air. | Pressure of $CO_2$ in mm. Hg in alveolar air at 37° saturated with moisture. | Rectal temperature, degrees Fahrenheit. |
|---|---|---|---|
| (1) Work of 1056 kg.m. per minute for 21 minutes. Bar. 757 mm. | | Cooled by two fans during work. | |
| Normal before start | 5·37 | 38·2 | 99 5 |
| 4′ after stop | 5·23 | 37·2 | |
| 11 ,, | 5·23 | 37 2 | |
| 18 ,, | — | — | 100·3 |
| 22¾ ,, | 5·13 | 36·4 | |
| 31½ ,, | 5·28 | 37·5 | |
| 47 ,, | 5·33 | 37·8 | |
| 58 ,, | — | | 98·9 |
| 61½ ,, | 5·50 | 39·1 | |
| 71 ,, | - | - | 98·7 |
| 77½ ,, | 5·46 | 38·8 | |
| (2) Work of 1056 kg.m. per minute for 20 minutes. Bar. 761 mm. | | Cooled by two fans during work. | |
| Normal before start | 5·52 | 39·4 | 99·2 |
| 4¾′ after stop | 4·87 | 34·8 | |
| 11¾ ,, | 5·07 | 36·2 | |
| 18 ,, | — | — | 99·9 |
| 21¾ ,, | 5·30 | 37·8 | |
| 32 ,, | | | 99·4 |
| 35¾ ,, | 5·24 | 37·4 | |
| 46 ,, | — | — | 99·0 |
| 50 ,, | 5·48 | 39·1 | |

after-effect on the alveolar $CO_2$ pressure, may tempt one at first sight to suggest that the lactic acid was mainly produced in the early period of the exercise, at a time, perhaps, when the circulation had not yet become fully adapted to meet the demand made on it owing to the sudden increase in the metabolism of the active muscles. This may be so, but it will be evident from what we have said previously that the figures as they stand do not justify this interpretation, for we might get a result of the same character if lactic acid were produced at a slow rate throughout the muscular work and elimination or destruction of lactic acid were gradually to balance its production. Under these circumstances, as the initial disturbance caused by the production of lactic acid dies away, a change in the respiratory quotient, due to an alteration in the character of the metabolism in the tissues, should gradually be unmasked, and, in the later periods of work in these experiments, any persistent increase of the respiratory quotient may well have the same explanation as the one we have already put forward in the case of lighter work, viz., an increase in the proportion of carbohydrate to fat metabolised. In order to settle the point clearly, the simplest plan would appear to be to eliminate so far as practicable any possibility of want of oxygen, and this could be done by working in an atmosphere containing a

higher percentage of oxygen than normal. Unfortunately, we have not yet had the opportunity of making these experiments.

Experiment 11 on HOBSON differs from the other experiments with this degree of work, as it resembles closely the result we got on DOUGLAS with work of 704 kg.m. per minute. The work leads to a rise of respiratory quotient, which diminishes progressively during the course of the work, but there is no definite evidence pointing to excessive hyperpnœa and washing out of pre-formed $CO_2$ in the early stages. Only a trace of lactic acid could be found in the urine at the end of the experiment, and this was probably not in excess of what is shown by normal urine. Apparently, therefore, HOBSON was not affected by any gross want of oxygen in this experiment, though, in Experiment 10, the additional demand of 200 c.c. of oxygen per minute, entailed by the disadvantageous conditions under which he was working, sufficed to put him in difficulties from this cause. Owing to HOBSON's better physical condition, one would naturally expect him not to show want of oxygen effects as soon as DOUGLAS.

If we discard in the experiments on DOUGLAS the early periods in which the respiratory quotients are clearly abnormally high, and confine ourselves to the last observation during work in Experiment 8, and the last three in Experiment 9, the average volume of each breath during the work is 2451 c.c., and the $CO_2$ percentage in the expired air 4·52 per cent. Assuming the resting effective dead space of 244 c.c. to hold good during the work, the calculated alveolar $CO_2$ percentage during the work becomes 5·01 per cent., a value which is considerably below the normal found at rest, but approximately the same as the temporary low value found shortly after the cessation of the work (Table IX). The average total ventilation of the lungs is 60·5 litres per minute, *i.e.*, about 52·5 litres above the resting value. In the case of hyperpnœa caused by breathing air containing $CO_2$, this increase would have been caused in DOUGLAS'S case by a rise of 1·47 per cent. above the normal alveolar $CO_2$ percentage. If we assume in the experiments on DOUGLAS, with work of 1056 kg.m. per minute, that the hyperpnœa, when it has steadied down after the preliminary disturbance due to lactic acid production, is proportional to the mass of $CO_2$ produced, and the respiratory centre reacts to the same degree to changes of $CO_2$ pressure as during rest, we should expect to find an average rise in the alveolar $CO_2$ percentage of 1·47 per cent., not above the resting normal value of 5·5 per cent., but above the lowered threshold value maintained during the work owing to the effects of want of oxygen. The only index of this latter figure is furnished by the low value of about 5·1 per cent., to which the alveolar $CO_2$ falls after the stop of the exercise, though very likely this is not so low as that which prevailed during the work. Supposing the real average alveolar $CO_2$ percentage during the work had been 5·1+1·47, viz., 6·57 per cent., the effective dead space calculated from this figure, the average volume of a breath, and the average $CO_2$ percentage in the expired air would become 761 c.c., a large figure admittedly,

but still by no means out of the way in comparison with the observations of ourselves, of HALDANE, and of HENDERSON and his colleagues, which we have quoted previously. Here, again, the anticipated rise of alveolar $CO_2$ pressure and the calculated volume of the dead space would have been considerably reduced during the work if a "direct" effect of oxygen deficiency on the respiratory centre had been superimposed upon the effects caused by lactic acid accumulation.

In HOBSON'S case, if we assume the resting dead space to remain constant during the work, his alveolar $CO_2$ percentage during the work (Experiments 10 and 11) would be about 5·48 per cent., *i.e.*, a little above his resting normal and a little below the alveolar $CO_2$ percentage calculated during the work of 704 kg.m. per minute.

(iii) *Work of* 1232 *kg.m. per Minute.*

The results obtained in the single determination made during the work are evidently an exaggeration of those observed in the earlier period of work in Experiments 8, 9, and 10. No less than 0·57 grm. of lactic acid was recovered from the urine passed at the end of the experiment. Though the hyperpnœa was still very excessive, the respiratory quotient was only 1·03 when it was determined just before the stop, but it is evident that it must have had a much higher value at an earlier stage of the work before a great part of the excess of preformed $CO_2$ had been blown off. It is most unfortunate that we were prevented from determining the respiratory exchange at the end of the first 4 minutes of the work, but we can get some idea of what might have been happening in the earlier stages from some previously unpublished observations of DOUGLAS, HALDANE, and BOOTHBY. These are shown in Table X.

TABLE X.

| Body weight in lbs. | Pace in miles per hour. | Kg.m. of lifting work per minute. | Respiratory exchange in c.c. per minute at 0° and 760 mm. | | Respiratory quotient. | Breaths per minute. | At 37°, moist, and prevailing barometer. | | $CO_2$ per cent. in expired air. |
|---|---|---|---|---|---|---|---|---|---|
| | | | $O_2$. | $CO_2$. | | | Litres breathed per minute. | C.c. per breath. | |
| DOUGLAS. | | | | | | | | | |
| 150 | 2·8 | 1132 | 2870 | 3490 | 1·22 | 11·4 | 109·4 | 2670 | 3·95 |
| -- | 2·7 | 1095 | 2940 | 3120 | 1·16 | 45·5 | 101·8 | 2300 | 4·01 |
| HALDANE. | | | | | | | | | |
| 183 | 2·5 | 1125 | 2790 | 3015 | 1·08 | 39·0 | 80·3 | 2060 | 4·64 |
| BOOTHBY. | | | | | | | | | |
| 113 | 1·6 | 570 | 2750 | 3300 | 1·20 | 39·0 | 96·1 | 2465 | 4·25 |

The work in this instance consisted in pushing a motor bicycle weighing about 150 lb. up an average gradient of 10·8 per cent., and the muscular work was continued for three minutes only before the sample of expired air was collected in a bag carried on the back of the subject, the collection of the sample taking rather over one minute. The walk was begun at a point where the gradient was far less steep and about one minute elapsed before the gradient of 10·8 per cent. was reached. The second experiment on DOUGLAS was made 1½ hours after the first. BOOTHBY started walking at too fast a pace to keep it up, and as he was slowing up very rapidly towards the end of the period of sampling owing to exhaustion, the average pace of 1·6 miles an hour does not give a real indication of the rate of work that he really reached during the observation.

These experiments were originally made simply to get some idea as to how far the respiratory exchange could be increased in really severe muscular work. The subjects were absolutely untrained, but BENEDICT and CATHCART'S observations show that a trained athlete can keep up work entailing an oxygen consumption of 3000 c.c. per minute, or even more, for some time. Judging by the oxygen consumption in DOUGLAS'S case the metabolism was perhaps a little higher than in Experiment 12, but the hyperpnœa and distress seemed to be much the same in the two cases. Respiratory quotients as high as 1·2 were reached, the volume of $CO_2$ produced per minute being in excess of the volume of oxygen absorbed by amounts varying in the different experiments from 225 c.c. in HALDANE'S case to 620 c.c. in the first observation on DOUGLAS. These figures give some idea what an enormous volume of preformed $CO_2$ may be expelled in very severe work. The excessive hyperpnœa and the lowness of the $CO_2$ percentage in the expired air are particularly marked in the experiments on DOUGLAS and BOOTHBY.

Further evidence regarding the cause of the very violent hyperpnœa, and the amount of preformed $CO_2$ that may have to be got rid of in short experiments when the work is extremely severe, is afforded by the observations of CHRISTIANSEN, DOUGLAS, and HALDANE (*loc. cit.*), in which it was shown that muscular work of this character led to an enormous temporary alteration in the $CO_2$ absorption power of the blood, the volume of $CO_2$ that can be held in combination in the blood at any given partial pressure of $CO_2$ being greatly reduced, as well as to a very great lowering of the threshold stimulating value of $CO_2$ on the respiratory centre, recovery of the normal absorption curve and normal threshold value of $CO_2$ not being attained till an hour or more after the stop of the muscular work.

(3) *The Respiratory Exchange during the Period of Rest following the Muscular Work.*

One of the most striking features in our experiments is the exceedingly rapid fall of both the respiratory exchange and the hyperpnœa as soon as the muscular exercise

stops. It has, of course, long been recognised experimentally* that such a fall occurs, though it is not till one can plot out the actual values as a continuous record that one fully appreciates its character. It is quite clear from figs. 4–7 that by far the greater part of this fall occurs in the first minute or two after the stop of the work, though a number more minutes elapse before the respiratory exchange and the hyperncea definitely fall to a steady value. The total period elapsing after the stop of the exercise before the respiratory exchange reaches a steady minimum varies in different experiments from 11 to 28½ minutes, with an average of about 20 minutes. We may presumably regard these final steady values as representing truly the more or less lasting effects produced on the resting respiratory exchange by a period of muscular work, and it seems reasonable to look upon the rapidly diminishing respiratory exchange in the period between the stop of the work and the assumption of these steady values as being determined, both in amount and character, by certain temporary causes incidental to the transition from work to rest.

The respiratory exchange after the stop of the muscular work is excessive for a short time in comparison with the figure at which it remains constant in the later stages, and it is of interest to ascertain the magnitude of this "excess respiratory exchange." This can be done in the case of some of our experiments in which the data are sufficiently complete by calculating the total respiratory exchange for the whole period from the stop of the work till the respiratory exchange reaches a reasonably steady value, and subtracting from the figure so obtained the total respiratory exchange calculated for the same period at the final steady rate. The figures are given in Table XI.

By comparison with Tables II–VI it will be seen that the "excess oxygen consumption" after work of 704 and 1056 kg.m. per minute on the average barely amounts to as much as the oxygen consumption during one minute of the muscular work, while the "excess $CO_2$ production" is considerably higher than the $CO_2$ production during one minute of the muscular work. In the case of the severe work of 1232 kg.m. per minute the "excess respiratory exchange" is greatly above the respiratory exchange during one minute of the previous muscular work. The values of this "excess respiratory exchange" after the work of 704 and 1056 kg.m. per minute are surprisingly low, especially as regards the oxygen consumption, but agree completely with the conclusions of earlier observers. LOEWY, for instance, states† that after the cessation of muscular work the respiratory exchange remains high for several minutes, though the excess oxygen consumption during the entire period of rest following the exercise scarcely amounts to so much as the oxygen consumption

* SPECK, 'Physiologie d. menschl. Atmens,' p. 56, Leipzig (1892); KATZENSTEIN, 'Pflügers Archiv,' vol. 49, p. 330 (1891); LOEWY, 'Pflügers Archiv,' vol. 49, p. 405 (1891); ZUNTZ und SCHUMBURG, *loc. cit.*, pp. 223, 235; ZUNTZ und HAGEMANN, 'Stoffwechsel des Pferdes,' p. 286, Berlin (1898).

† *Loc. cit.* See also LOEWY, 'Oppenheimer's Handbuch der Biochemie,' vol. 4, Part 1, p. 262, Jena (1911).

during a single minute of the work period, and only mounts to a higher value when there is great muscular fatigue or when the work is done under conditions of insufficient supply of oxygen.

TABLE XI.

| Experiment. | Work in kg.m. per minute. | Final period after the work in which the respiratory exchange is steady. | | | Period intervening between the stop of the work and the assumption of the steady respiratory exchange. | | |
|---|---|---|---|---|---|---|---|
| | | Length of period. | Average respiratory exchange in c.c. per minute. | | Length of period. | Total $O_2$ consumption and $CO_2$ production in c.c. in excess of values which would have been obtained if the respiratory exchange during this period has been the same as the steady rate eventually reached. | |
| | | | $O_2$. | $CO_2$. | | $O_2$. | $CO_2$. |
| DOUGLAS. | | | | | | | |
| 2 | 704 | 33′ 37″ | 297 | 230 | 21′ 2″ | 1775 | 2262 |
| 3 | 704 | 33 31 | 298 | 234 | 18 3 | 1598 | 1807 |
| 8 | 1056 | 25 6 | 287 | 222 | 17 58 | 2512 | 3543 |
| 9 | 1056 | 68 37 | 328 | 248 | 10 56 | 1880 | 2720 |
| 12 | 1232 | 57 4 | 308 | 204 | 28 27 | 3708 | 5981 |
| HOBSON. | | | | | | | |
| 4 | 704 | 21 55 | 342 | 300 | 20 35 | 1363 | 1650 |
| 11 | 1056 | 32 55 | 350 | 285 | 24 30 | 2068 | 2498 |

Several different factors must combine to prevent the respiratory exchange from falling to a steady resting value immediately after the work stops, and some of these suggest themselves at once.*

(i) At the moment when the muscular work stops, blood, whose gaseous content has been determined by the last few moments of muscular activity, is in process of passing from the active muscles to the lungs. Clearly there can be no material decrease in the gaseous exchange in the lungs till the last of this blood has passed through the lungs.

(ii) It is improbable that at any given moment in the course of muscular activity the gaseous content of the blood leaving the active muscles corresponds with the actual consumption of oxygen or formation of $CO_2$ at the same moment in these muscles. The changes in the blood must lag a little behind the changes in the muscles, partly on account of the time required for the passage of gases between the blood and the muscles, and partly perhaps on account of the nature of the processes involved in the absorption of oxygen and production of $CO_2$ in a muscle.† At the

* In this connection see DURIG und ZUNTZ, 'Skand. Archiv für Physiol.,' vol. 29, p. 133 (1913).

† See FLETCHER and HOPKINS, 'Roy. Soc. Proc.,' B, vol. 89, p. 444.

same time it would appear that a lag of this description must be a pretty small thing under normal conditions of activity with an effective circulation of the blood through the muscles, otherwise it is difficult to see why it would not act prejudicially if the work were to be kept up for more than a short time, though the lag will be somewhat accentuated in the case of $CO_2$ by the capacity of the blood and tissue fluids for absorbing more $CO_2$ at higher partial pressures of the gas.

(iii) It is possible that complete rest is not assumed at once on stopping the work, or the "tone" of the muscles may only decrease gradually to a steady value after a period of activity. When determining the resting respiratory exchange it is always necessary to wait for some time before a reasonably steady value can be obtained, even if the preceding activity has been quite slight.

(iv) General rise of body temperature causes an increase of the resting metabolism.* When, therefore, rest is resumed after a period of muscular activity one would expect the metabolism in those parts of the body in which the exercise has caused a rise of temperature to remain unduly high until the temperature falls back to its normal value.

(v) The hyperpnœa after the stop of the muscular exercise decreases in much the same manner as does the respiratory exchange, keeping pace with $CO_2$ production rather than with oxygen consumption. So long as the hyperpnœa persists it implies some increase in the resting metabolism on account of the heightened activity of the respiratory muscles.

Of these factors, the first, which would have a considerable effect, as well as the second, one would expect to be limited to a brief period after the stop of the work, whereas the last three would be operative for a longer period and would cease more gradually. The excess respiratory exchange per minute in our experiments is far greater in the first period after the stop than in any of the subsequent periods, and after the great primary fall diminishes more and more gradually as the final steady value of the respiratory exchange is approached.

The fact that there is a temporary sharp rise of the respiratory quotient to 1·0 or beyond, *i.e.*, that the $CO_2$ output is for a brief time actually in excess of the oxygen absorption, immediately after the stop of the exercise has been noticed by other observers (Loewy, Katzenstein, Zuntz and Hagemann, Zuntz and Schumburg; *loc. cit.*). These authors have suggested that the cause of this is to be found in the fact that in addition to $CO_2$ other substances derived from the active muscles (*e.g.*, lactic acid) stimulate the respiratory centre, and that on cessation of the work the breathing remains exaggerated until these substances can be oxidised, the exaggeration of the breathing implying, of course, washing out of $CO_2$ from the body in excess of the oxygen absorbed.

This theory alone seems to us quite insufficient to explain the facts. The sharp rise of the respiratory quotient is shown in our experiments no matter whether the

* Sutton, 'Journ. Path. and Bact.,' vol. 13, p. 62 (1909).

work is light or heavy, or the period of exercise short or long, though the rise is more marked in the experiments with work of 1056 kg.m. per minute than in those with work of 704 kg.m. per minute. We have shown above that we could get no distinct evidence of the formation of lactic acid in the case of work of 704 kg.m. per minute. In the experiments with work of 1056 kg.m. per minute we got unmistakable evidence of the formation of lactic acid in several cases; the amount, however, did not appear to be very great, while it seemed quite likely that in the later stages of the work production and elimination of lactic acid were balanced. In neither of these cases does there seem to be any reason for supposing that $CO_2$ would be expelled from the body after the stop of the work out of proportion to the oxygen consumed.

The facts seem to us capable of another interpretation. Whilst admitting that there will no doubt be a tendency during the work to accumulation of $CO_2$ in the active parts of the body owing to the amount of $CO_2$ held in the blood and tissue fluids being dependent on the partial pressure of $CO_2$, and that this excess will be given off directly the work stops, the close similarity both in general character and in rate between the diminution of the hyperpnœa after stopping the work and the diminution of the hyperpnœa when breathing is resumed after holding the breath,* or when fresh air is breathed again after exposure to an atmosphere containing $CO_2$†, suggests the necessity of a deeper explanation. In the latter two cases the difficulty was pointed out of explaining the gradual subsidence of the hyperpnœa without any signs of marked periodicity of the breathing, unless the assumption was made that the respiratory centre is itself charged up with more $CO_2$ than normal in consequence of the rise of alveolar $CO_2$ pressure while the breath is held or air containing $CO_2$ is breathed, and that the washing out of this excess from the respiratory centre when the breathing recommences or fresh air is again breathed takes an appreciable time.

It appears to us probable, therefore, that the alveolar $CO_2$ pressure during the work is above the resting threshold stimulating value which holds good just after the exercise stops—this may be the same as the normal threshold value in the case of light work, or lower than the normal in the case of heavy work owing to the effect of lactic acid (and perhaps rise of temperature), and that $CO_2$ is therefore dammed back in the body at large, including the respiratory centre, during the work. It has been shown above that this condition can only be attained in our experiments if the effective physiological dead space during the hyperpnœa is increased during the work above the normal resting value. Directly the muscular work ceases the alveolar $CO_2$ pressure will tend to fall as $CO_2$ production is reduced, and the $CO_2$ which was dammed back in the body will be expelled, the expulsion being rapid at first while the excess of $CO_2$ retained in the body is still high, and then becoming slower and slower as the amount of $CO_2$ retained sinks towards the value corresponding to the prevailing threshold $CO_2$ pressure. Expulsion of $CO_2$ dammed back in this manner

* Douglas and Haldane, *loc. cit.*

† Campbell, Douglas, Haldane, and Hobson, *loc. cit.*

would not be accompanied by any corresponding variation in the oxygen consumption. One would expect that the higher $CO_2$ production in the heavier work experiments would be accompanied by a higher relative increase in the alveolar $CO_2$ pressure than is the case with the lighter degree of work, and this will help to explain why the sharp rise of the respiratory quotient after the stop of the work is more pronounced with work of 1056 kg.m. per minute than it is with work of 704 kg.m. per minute.

If, however, the body has not attained equilibrium with the lactic acid production by the time the work stops, it is evident that the action of lactic acid must continue during the earlier period of rest following on the muscular exercise, and that its effect will be superimposed on that postulated above. This condition must be present in Experiment 12 at least, for as the respiratory quotient was still above unity in the last period of work it is clear that the expulsion of preformed $CO_2$ was not by any means complete when the work stopped, and this process must have continued for some time after resuming rest.

The precise height to which the respiratory exchange will rise after the exercise stops will depend in observations of this type on the length of the period of observation, for the longer the period the lower must be the apparent rise. At the same time one would expect the rise to be most evident not in the first few moments after the stop of the work, when the gaseous content of the blood reaching the lungs is still largely determined by the gaseous exchange of the muscles in the final stage of of the work, but at a slightly later period when the respiratory exchange has dropped considerably. This seems to be the case in Experiment 12, where the highest respiratory quotient was observed not in the first 51 seconds after the subject resumed rest, but in the succeeding period of 1 min. 37 secs.

It would be of very great interest to ascertain the amount of surplus $CO_2$ which is expelled without corresponding intake of oxygen in the early period after the stop of the exercise, but our data are insufficient for this purpose, though it is possible to get some idea as to the order of magnitude of this quantity. It would no doubt be right to regard the volume of $CO_2$ produced in excess of the total volume of oxygen absorbed whilst the respiratory quotient is above unity as derived from $CO_2$ dammed back or preformed in the body, and to take this as the minimal value. During this time, as well as in the subsequent two or three periods, there is, however, nothing to indicate the true respiratory quotient significant of the character of the metabolism in the tissues as distinct from the observed respiratory quotient, which must differ from the former in a degree depending on the amount of surplus or preformed $CO_2$ expelled or on the amount of $CO_2$ retained to make up for a deficiency previously created. It would seem to us that a still fairer approximation would be obtained by taking the whole period following the stop of the muscular work in which the respiratory quotient is above the value found in the last work period, and reckoning as surplus $CO_2$ expelled from the body the volume of $CO_2$ in excess of what is required by the oxygen intake if one allows a respiratory quotient identical with that shown in the

last work period. The real metabolic respiratory quotient directly after the work can hardly exceed that shown during the last stages of the work; in fact, the general course of events would suggest that it begins to fall very soon after the exercise stops. We can obtain a limiting value for this surplus $CO_2$ discharge by assuming that the real metabolic respiratory quotient falls immediately after the stop of the work to its final steady value, and calculating the excess $CO_2$ on this assumption for the whole period which elapses before the respiratory exchange and observed respiratory quotient become steady, for such a value must be in excess of the true one since the respiratory exchange and metabolic respiratory quotient are bound to approximate in the first few moments after the stop to the values shown during the last stages of the work, while no account is taken of the possibility that the fall of the respiratory quotient may be in part attributable to retention of $CO_2$. The values calculated by these three methods are given in Table XII, and it will be seen that with the exception of Experiment 11 the apparent surplus of $CO_2$ expelled is greater after the heavier work than after the lighter.

TABLE XII.

| Experiment. | Work in kg.m. per minute. | Surplus $CO_2$ production after the stop of the work in c.c., reckoned on the assumption that it indicated so long as the respiratory quotient is above :— | | |
|---|---|---|---|---|
| | | 1·00 | Value shown in last period of work. | Final steady value shown in later periods of rest. |
| DOUGLAS. | | | | |
| 2 | 704 | 114 | — | 882 |
| 3 | 704 | 132 | 322 | 557 |
| 5 | 704 | 20 | 354 | — |
| 6 | 704 | — | 253 | — |
| 8 | 1056 | 540 | 678 | 1598 |
| 9 | 1056 | 380 | 570 | 1290 |
| 12 | 1232 | 620 | — | 3531 |
| HOBSON. | | | | |
| 4 | 704 | 106 | 296 | 115 |
| 7 | 704 | 63 | 287 | — |
| 10 | 1056 | 272 | 620 | — |
| 11 | 1056 | 90 | 302 | 818 |

One slight source of error in our results may be alluded to here, since it is likely to be most evident just after the work stops. The bag method can only give a perfectly correct result provided that the composition of the air left in the lungs at the end of the period of sampling is identical with that at the beginning. This condition is fulfilled in the normal resting condition or when the subject is in equilibrium with the work. If, however, the composition of the air in the lungs alters while the expired

air is collected an error is introduced in the calculation of the $CO_2$ output and oxygen absorption. Thus if the $CO_2$ percentage in the air in the lungs is lower at the end of the period than it was at the beginning, a change which is likely to occur when rest is resumed after a period of work, the contents of the bag will indicate a rather higher $CO_2$ production and oxygen consumption than the true respiratory exchange of the body at the time. Our periods of sampling were, however, so long, and the total $CO_2$ production and oxygen consumption during the period so large, that any error due to this cause becomes negligible, the more so as the chest is in the expiratory position when the period begins and when it ends, and the volume of air contained in it is therefore small. Change of respiratory quotient in the air in the lungs might also cause a slight error in the observed respiratory quotient, but having regard to the general rate at which the respiratory quotient alters in our experiments this error would be quite trivial.

It will be seen in Tables II and III that the respiratory exchange and respiratory quotient eventually fall back after the stop of the work of 704 kg.m. per minute to just about the same values as were shown during the preliminary rest (see also Table XIII below). In DOUGLAS's case there is some evidence that the respiratory quotient falls to a minimal value, which is slightly below the original resting value, about 20–30 minutes after the stop of the exercise, and may then rise again to the

TABLE XIII.

| Experiment. | Work in kg.m. per minute. | Preliminary resting period. | | | Final steady period after the work. | | |
|---|---|---|---|---|---|---|---|
| | | Respiratory exchange in c.c. per minute. | | Respiratory quotient. | Respiratory exchange in c.c. per minute. | | Respiratory quotient. |
| | | $O_2$. | $CO_2$. | | $O_2$. | $CO_2$. | |
| DOUGLAS. | | | | | | | |
| 1 | 704 | 286 | 227 | 0·793 | — | — | — |
| 2 | 704 | — | — | — | 297 | 230 | 0·775 |
| 3 | 704 | — | — | — | 298 | 234 | 0·785 |
| 5 | 704 | 294 | 239 | 0·813 | — | — | — |
| | | 293 | 231 | 0·788 | | | |
| 6 | 704 | 263 | 213 | 0·808 | 269 | 212 | 0·788 |
| 8 | 1056 | 281 | 233 | 0·829 | 287 | 222 | 0·773 |
| 9 | 1056 | 308 | 266 | 0·863 | 328 | 248 | 0·756 |
| 12 | 1232 | — | — | — | 308 | 204 | 0·662 |
| HOBSON. | | | | | | | |
| 4 | 704 | 385 | 331 | 0·860 | 342 | 300 | 0·877 |
| | | 350 | 308 | 0·880 | | | |
| 7 | 704 | — | — | 0·866 | — | — | — |
| 10 | 1056 | 394 | 349 | 0·885 | — | — | — |
| | | 423 | 373 | 0·881 | | | |
| 11 | 1056 | 375 | 323 | 0·860 | 350 | 285 | 0·815 |

preliminary resting value. This apparent variation in the respiratory quotient depends, however, on such small differences in the observed values of $CO_2$ output and oxygen consumption that it becomes rather dubious. There is certainly no marked diminution of the respiratory quotient which we should have expected if the rise of the respiratory quotient during the work had been due to expulsion of preformed $CO_2$, and had been followed after the stop of the work by retention of a corresponding amount of $CO_2$. The absence of this feature supports the view, therefore, that the rise of the respiratory quotient during the work is in this case due to a relatively greater employment of carbohydrate.

After work of 1056 kg.m. per minute, the respiratory quotient falls quite definitely below the preliminary resting value. In DOUGLAS'S case this fall is more obvious in Experiment 9 than in Experiment 8, in which the work lasted for a much shorter period; it is also more marked than in Experiment 11 on HOBSON, notwithstanding the long period of work in this case. This is shown in Table XIII, which gives the preliminary resting respiratory exchange and the average respiratory exchange during the later period after the stop of the work when a fairly steady value is reached in the different experiments.

In Experiment 8 the oxygen consumption during the final steady period is on the whole slightly above, and the $CO_2$ production slightly below, corresponding values in the preliminary resting period. In Experiment 9 the alteration is in the same sense, but much more marked. In Experiment 11, however, both oxygen consumption and $CO_2$ production are lower than in the preliminary resting period, though the diminution of $CO_2$ production is proportionally greater than that of oxygen consumption. In Experiments 8 and 9 there was definite evidence of lactic acid formation and expulsion of preformed $CO_2$ during the work, and one might therefore expect that gradual retention of $CO_2$ after the work would account either in whole or part for the lowering of the respiratory quotient.

In our observations on the alveolar air changes, after this degree of work, we found (Table IX) that the aveolar $CO_2$ pressure reached the lowest point between the 4th and the 20th minutes after the stop of the work, and that recovery of the normal alveolar $CO_2$ pressure occurred within $\frac{3}{4}$ to 1 hour. As observations were only kept up for 43 minutes after the stop of the work in Experiment 8, retention of $CO_2$ might easily be sufficient to account for the lowering of the respiratory quotient. In Experiment 9, however, there is no definite indication of a gradual rise in the respiratory quotient, though observations were kept up for 79 minutes after the stop of the work, nor does Experiment 11 differ in this respect, though in this instance there were no variations in either the hyperpnœa or $CO_2$ output during the work, significant of lactic acid production. In BENEDICT and CATHCART'S experiments a low respiratory quotient was also observed after exercise, and this was in some cases found to persist for as much as several hours.

It is therefore far from probable that the sole cause of the low respiratory quotient

after work in these last two experiments is $CO_2$ retention, and what appears to us more likely is that some at least of the diminution is due to the fact that when rest is resumed proportionally less carbohydrate than fat is metabolised than in the preliminary resting period owing to the depletion of carbohydrate during the work, a suggestion which is in consonance with the views expressed by the Zuntz school and by BENEDICT and CATHCART. It is, however, rather a remarkable feature that the fall of respiratory quotient after the stop of the work only becomes obvious in the experiments with work of 1056 kg.m. per minute, though Experiment 6 with work of 704 kg.m. per minute actually led to a greater total output of energy, owing to the longer duration of the work. In the experiments at 1056 kg.m. per minute, however, the work was done at a greater rate, and the average respiratory quotient was at a higher level during the work, so the actual effect on carbohydrate metabolism may have been greater. At first sight, one is liable to suggest that the high oxygen consumption in the final steady period of Experiment 9 may indicate some transformation of fat into carbohydrate to make up for the depleted stores of the latter, for this would entail some oxygen consumption without corresponding $CO_2$ production. Against this is the fact that in our experiments the energy output (calculated by the Zuntz-Schumburg Tables) is practically identical in the preliminary resting period and in the final stages of the rest following the work: *e.g.*, in Experiment 9 the calorie output per minute during the preliminary rest is 1·50 calories, and during the final steady period after work 1·55 calories, and in Experiment 8 these figures are 1·36 and 1·37 respectively.

In Experiment 12 with very severe work of 1232 kg.m. per minute the respiratory quotient falls to a very low value in the later stages of rest following the exertion, and for the last 57 minutes of the experiment is well below 0·7. The $CO_2$ output during the whole of this period is extremely low, especially if one considers it in relation to the oxygen consumption, and there seems little doubt that this is mainly determined by retention of $CO_2$ to make up for the large quantity of preformed $CO_2$ expelled at an earlier stage of the experiment. The average oxygen consumption during this period is rather higher than in the majority of the experiments, but this is mainly due to the high values in the last two determinations, and it is possible that these indicate a rise in the general metabolism owing to some accidental cause, *e.g.*, the subject may have got rather cold from sitting still so long (the period of rest after the work lasts in this case for almost an hour and a half). That $CO_2$ retention should continue for so long after the stop of the exertion is not in itself surprising, considering the severity of the work and the magnitude of the lactic acid effect, for, after exertion of similar severity (due to running up and down stairs repeatedly), CHRISTIANSEN, DOUGLAS, and HALDANE found (*loc. cit.*) that the alveolar $CO_2$ pressure was in one case still distinctly below the normal value 70 minutes after the work stopped, and the absorption power of the blood for $CO_2$ still depressed. The whole course of events in this experiment is very much like that observed by

Douglas, Haldane, Henderson, and Schneider (*loc. cit.*) in the Pikes' Peak expedition after ascending a quarter of a mile of a 1 : 4 gradient in 5 minutes at an altitude of 14,000 feet. This led to a great lowering of the respiratory quotient after the stop, the diminution being due to reduction of $CO_2$ output rather than to alteration in oxygen consumption. The respiratory quotient reached its minimum on this occasion half to three-quarters of an hour after the stop, and then rose slowly again, though a normal respiratory quotient was reached within an hour and a half in only one experiment.

It will be seen from Tables II–VI that in Experiments 4 and 6 the $CO_2$ percentage in the expired air and the depth of the breathing are about the same both in the preliminary resting period and in the last steady period after the stop, and that in Experiment 11 lowering of the expired $CO_2$ percentage in the later periods of the experiment is accompanied by a diminution in the depth of the breathing. In none of these cases does there seem to be any material alteration in either the dead space or the alveolar $CO_2$ percentage. In Experiment 9, and especially in Experiment 8, there is, however, a marked diminution in the expired $CO_2$ percentage in the final steady period after the stop below the value shown in the preliminary resting period, though the depth of the breathing remains much the same. This must indicate either an increase in the dead space or a lowering of the alveolar $CO_2$ pressure below their preliminary resting values. From the observations given in Table IX, one would not have expected a lowering of the alveolar $CO_2$ pressure to have lasted so long, or to have been of such magnitude, as to have made so great and lasting a difference in the expired $CO_2$ percentage, though it is true that the minimum percentage of $CO_2$ in the expired air is reached in Experiment 9 during the period when we might have expected the alveolar $CO_2$ pressure to be at its minimum. In Experiment 12 again the fall in the expired $CO_2$ percentage is more than can be accounted for by the small depth of the breathing, though in this case there is every reason to suppose that the alveolar $CO_2$ pressure was a good deal below the normal value. We feel, however, that further investigations are necessary on this point before a definite opinion can be formed.

A good deal more work is obviously necessary before we can get a clear picture of the course of events in these comparatively short periods of muscular work. The problem which appears to need most urgent solution is the part played by want of oxygen, for our present knowledge is still very inexact in this respect. It is evident that caution must be used in reckoning the energy output during short periods of hard muscular work, as well as during the earlier stages of rest following on the work, since the respiratory quotient is liable to show large temporary alterations which are dependent on other factors than an alteration in the proportion of carbohydrate to fat metabolised, such alterations involving great variations in $CO_2$ output without corresponding variations in oxygen consumption.

*Conclusions.*

(1) A simple method is described which enables a practically continuous record to be obtained of the respiratory exchange and hyperpnœa during and after muscular work on a stationary ergometer. It is possible by this means to get a considerable amount of information regarding rapid and transitory variations in the respiratory exchange.

(2) The efficiency of the body determined by this method agrees closely with the results obtained by other observers.

(3) Evidence is given in favour of the view that muscular work not infrequently involves the metabolism of a higher proportion of carbohydrate to fat than is the case during rest.

(4) With the harder degrees of work the course of events is liable to be influenced by the effects of serious shortage of oxygen as indicated by the production of lactic acid, which leads to a temporary great exaggeration of the hyperpnœa, accompanied by washing out of preformed $CO_2$ from the body and an abnormally high respiratory quotient. Our experimental data are not sufficient to exclude the possibility of the action of a slight degree of oxygen deficiency (possibly a "direct" action on the respiratory centre) in the lighter degrees of work in which there is no definite evidence of the production of lactic acid.

(5) After the stop of the work the respiratory exchange and hyperpnœa diminish with great rapidity. The respiratory quotient shows an immediate, but quite temporary, sharp rise, and it is suggested that this is largely due to the expulsion of $CO_2$ dammed back in the body during the muscular work owing to the alveolar $CO_2$ pressure being above the threshold stimulating value for the respiratory centre which prevails just after the cessation of the work, though this effect may be exaggerated by the simultaneous action of lactic acid. After this the respiratory quotient may return to the same value that it had previous to the muscular work, or it may show a marked diminution indicative of retention of $CO_2$ to make up for the preformed $CO_2$ washed out of the body at an earlier stage, or of a true change in the tissue metabolism dependent on the depletion of carbohydrate during the work.

The expenses in connection with much of the apparatus used in this research have been defrayed by a grant from the Royal Society, to whom we desire to express our thanks.

# II.—*The Microscopical Features of Mechanical Strains in Timber and the Bearing of these on the Structure of the Cell-wall in Plants.*

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[PLATES 1–4.]

## INTRODUCTION.

When wood is subjected to increasing mechanical stress its component parts ultimately undergo changes resulting in permanent deformation or failure.* This paper deals with the minute microscopic changes upon which the permanent deformation of wood depends, and with the relationship between the microscopic structure of wood and some of its more important mechanical properties. The work has provided abundant material for a study of the structure of the walls of the cells of which wood is composed. Considerable light has been thrown on the structure and properties of the vegetable cell-wall in general, and it has been possible, from the facts for wood, to frame a hypothesis which seems to explain satisfactorily most of the properties of cell-walls.

The examination of the mode of failure in timber, which has led to the work described in this paper, was begun at the request of Lt.-Col. JENKIN, R.A.F. I am deeply indebted to him for the original suggestion of this line of work and for his continued interest during its course. I have derived great advantage throughout the work by discussing various engineering questions, as they have arisen, with Major ROBERTSON, R.A.F., and I desire to thank him for many helpful suggestions. I am further indebted to him for the supply of many fractured specimens of wood. The research has been carried out, in the course of more definitely applied work for the Air Ministry, in the Barker Cryptogamic Research Laboratory of the University of Manchester. I have to thank Prof. W. H. LANG, F.R.S., for encouraging me to attempt to relate the facts of the mechanical properties of wood to fundamental botanical questions bearing on the structure of cell-walls in plants.

The mechanical properties of a wood may depend on the microscopic or ultra-microscopic structure of the substance of the walls of the cells comprising it, on the form of these cellular elements, and also on their gross anatomical arrangement.

* It is recognised that a long thin column of wood may undergo mechanical failure by elastic instability, but since the deformation in such cases occurs within the limits of elasticity and is not permanent, the failure is accompanied by no permanent microscopical changes in the cell-walls of the wood. In this paper it is the changes accompanying failure by permanent deformation which are being considered.

In the present study it was found that the gross manner of failure in end-compression of some of the lighter coniferous woods differed in a striking way from that seen in many of the denser woods, both of Dicotyledons and of Conifers. It is probable that these gross differences are dependent on anatomical differences in the various woods, and are especially connected with the greater or smaller proportion of thick-walled elements, as well as with the form of the cells in the latter. On the other hand it is shown below that, underlying the gross differences in the manner of failure in end-compression in the various woods, there is a fundamental similarity in the method by which failure is initiated in the cell-walls of all woods. The earliest recognisable stages in the failure, due to the permanent deformation of the walls of the cells of the wood, are microscopic, and (requiring to some extent, special methods of demonstration) have not previously been described.

The macroscopic as well as some microscopic features of the failure of wood have been described by a number of investigators and brief reference must be made to the main results of their work.

THIL* (1900) described the anatomical structure of many woods in relation to their mechanical properties. He concluded that the form of the fracture depended on the medullary rays acting as places of less resistance and attempted to relate the course of the fracture to a spiral arrangement of the medullary rays.

JACCARD† (1910) investigated the anatomical structure of a large number of woods after compression. He studied the wood both of Dicotyledons and of Conifers and concluded that there is no specific type of rupture common to all woods and, contrary to THIL, that the fracture bears no relation to the medullary rays. The rupture is determined by points of least resistance in the wood, the pits in the walls of the tracheides and fibres forming such points of weakness. JACCARD described certain alterations in the folded cell-walls. He states that these show a longitudinal fibrillar structure which, in transverse sections, appears as a concentric layering in the walls. He attributes the appearances to the layers of the cell-walls having planes of less cohesion between them; under compression these planes behave as planes of cleavage and separation takes place along them. In the tracheides of the autumn wood of certain Conifers a fine transverse striation is referred to, but its significance is not discussed. Mention is also made of the similarity of some of the transverse folds he observed, to the dislocations described by VON HÖHNEL‡ for flax and other fibres.

FULTON§ (1912) studied the failure of Oak, Pitch Pine, Ash and Box, giving

* THIL, A., "Constitution anatomique du Bois."—'Étude sur les Fractures des Bois dans les Essais de Résistance.' 'Études présentées au Congrès Internat. des Méthodes d'Essai des Matériaux de Construction,' Paris, 1900. (Seen summarised in 'Le Bois,' Beauverie, 1905.)

† JACCARD, P., "Étude anatomique des Bois comprimés," 'Mitt. d. Schw. Centralanstalt für d. Forst. Versuchwesen,' vol. 10, heft 1, pp. 53–101, Zurich, 1910.

‡ HÖHNEL, VON, 'Jahrb. für Wiss. Bot.,' 1884, p. 311.

§ FULTON, A. R., "Experiments to show how Failure under Stress occurs in Timber, its Cause, etc.," 'Trans. Roy. Soc. Edin.,' vol. 48, Part II, p. 21 (1912).

illustrations of the external and of some microscopic characters of the failures he obtained. The manner of failure of specimens fractured in compression, in tension, and by bending was investigated, and FULTON concluded that "the initial cause of failure in all timber lies in the medullary rays." This failure is attributed to an initial set caused by the natural sinuous displacement of the fibres in a tangential plane round the medullary rays, and by the lack of cohesion between the fibres and the medullary rays. No details of any internal microscopic changes in the substance of the woody walls are given.

BRUSH* (1913) investigated the behaviour of the fibres of ten species of wood, in compression, tension, longitudinal shearing and bending. He found that for end-compression the fibres behave as hollow tubes and either buckle sharply or bend gradually. Whether a fibre buckles or bends depends on the thickness of its walls and on the moisture-content. Apart from this distinction between buckling and bending,† no description is given of more minute changes in the structure of the walls. No reference is made to the part played by the pits nor is the effect of the medullary rays considered.

RECORD‡ has summarised the results obtained by JACCARD and BRUSH but adds nothing to their descriptions.

## MATERIAL, METHODS, ETC.

Preliminary observations indicated that the problems involved in the mechanical failure of wood could be best elucidated by a detailed study of a few woods of different types. For the purpose of this investigation, therefore, the woods of Silver Spruce (*Picea sitchensis*), Ash (*Fraxinus excelsior*), and Pitch Pine (*Pinus palustris*) were selected. For the elucidation of special points and for the verification of the main conclusions of this paper a number of other woods including Mahogany, Swamp Cypress, Oregon Pine, Larch, Birch and also Andaman Padouk have been examined.

The mechanical stress which has been mainly considered is longitudinal compression, *i.e.*, compression applied endwise and therefore acting in the direction of the grain of the wood. In addition, longitudinal tension and longitudinal shearing, both in radial and tangential planes, were considered for comparative purposes. Short rectangular test-specimens were used in the earlier stages of the research, but for most of the work on the effect of longitudinal compression, small cylindrical test-specimens with expanded flanges at either end were prepared. These specimens measured 1 inch long by $\frac{1}{4}$ inch diameter at the narrowest portion. The end-compression was applied in a small testing machine designed and constructed for the purpose by Major

* BRUSH, W. D., "A Microscopic Study of the Mechanical Failure of Wood," 'U.S. Depart. Agric. Review Forest Service,' vol. 2, pp. 33–38 (1913).

† In the present paper the terms "crinkling" and "buckling" are respectively equivalent to BRUSH'S "buckling" and "bending."

‡ RECORD, S. J., 'The Mechanical Properties of Wood,' New York, 1914.

Robertson, R.A.F., to whom I am also indebted for the design of the test-specimen. The shape of the test-piece ensured that failure should occur in a middle region.

The shape of the specimens fractured in tension and in longitudinal shear, and also the method of test adopted in the latter case, are dealt with in the sections of the paper concerned with tension and with longitudinal shear.

True radial and tangential longitudinal sections were cut through the pieces after failure, and prepared for microscopical examination in the usual way. In order to retain the tissues and cells of the wood in the condition in which they were on removing from the testing machine and to prevent, as much as possible, expansion and readjustments in the tissues and cell-walls, the use of water was in most cases entirely avoided. The sections were cut from specimens soaked in absolute alcohol and the stains used were applied in solution in absolute alcohol. In using reagents like chlor.-zinc-iodide such treatment was not possible, but, by comparison with sections which were never wetted with water, it was possible to make allowance for the swelling and readjustment which took place.

## Gross Features of Compression Failure.

The gross appearances accompanying the compression failure in Spruce, Pitch Pine, and Ash will first be briefly described and then the detailed microscopic features of the failure will be dealt with for these woods.

In Spruce, after compression, a distinct zone of failure can be observed with the naked eye on both radial and tangential faces of a rectangular test-specimen. Plate 1, fig. 1, shows the appearance of the narrow zone of failure on the tangential face of such a compressed specimen. The zone is slightly inclined to the horizontal, its two edges are parallel, and there is no obvious displacement of the elements of the wood in the tangential direction as seen on this face. Plate 1, fig. 2, shows the zone of failure on the radial face of the same specimen. In this case the zone is practically horizontal, but its edges form a gently undulating outline. There is a most obvious displacement in the radial direction, this having been produced by the pushing over of the autumn wood of one year into the spring wood of the next. In some examples the displacement was so great that a separation of the tracheides took place at the annual rings (Plate 1, fig. 5*r*). The thin-walled tracheides of the spring wood in the zone of failure are crinkled and thrown into folds, whilst the thick-walled tracheides of the late wood are buckled more gradually. These differences, in the gross expression of the failure in the two kinds of tracheides, account for the undulating outline of the zone of failure which has been referred to above. In Spruce, there is no rupture between the medullary rays and the tracheides, nor indeed is any rupture visible on the tangential face of a compressed specimen. It will be seen later that Spruce differs in this particular from Pitch Pine, from Ash, and also from many of the woods, the failure of which has been described by the investigators referred to above.

In Pitch Pine, the zone of failure, as seen on a tangential face, is inclined at an angle of about 45° to the longitudinal axis of the specimen, the displacement of the elements of the wood having taken place in the tangential direction (Plate 1, fig. 3). The medullary rays are not of uniform size in Pitch Pine, and the separation takes place at the larger rays first (Plate 1, fig. 4). Owing to this separation at the medullary rays it is only possible to study the failure from tangential sections, since radial sections, except of specimens in very early stages of failure, separate completely into two parts. As in Spruce, the failure is manifested by buckling of the walls of the autumn wood and by crinkling of the walls of the spring wood. The proportion of thick-walled late wood, however, is much greater in Pitch Pine than in Spruce, and this probably accounts for the gross differences in the manner of failure.

In Ash, the gross features of the compression failure somewhat resemble those seen in Pitch Pine. The zone of failure is inclined at an angle, which may vary from 60° to 45°, to the longitudinal axis of the specimen. The failure manifests itself by the gradual buckling of the fibres, and this is accompanied by a displacement of the elements of the wood in the tangential direction (Plate 1, fig. 6). As in the failure of Pitch Pine, a separation of the elements ultimately occurs at the medullary rays. In Ash the fibres of the late wood comprise the main mechanical elements of the wood. When, therefore, a test specimen is compressed, the deformation of these fibres is responsible for the collapse of the specimen. As in Pitch Pine, the proportion of the thick-walled mechanical cells in the wood is very high when contrasted with a wood like Spruce.

These observations, on the grosser features of the failure of Pitch Pine and of Ash, confirm the descriptions given by FULTON for these two woods, but, as will be seen below, the present paper is not in agreement with his interpretation of the cause of failure. In Spruce, even the gross features of the failure are not in agreement with FULTON'S explanation, since the displacement is in the radial direction and separation never occurs at the medullary rays. It has been found that the actual causes of failure must be traced back to the initial stages of deformation which become manifest in the cell-walls of the tracheides, or fibres of the wood. This is the case, even though the final, grosser characteristics of the failure in woods like Pitch Pine and Ash, may partly be determined by the size and distribution of the medullary rays. From the results described below, it is likely that in all woods these initial stages of the failure and their relations to the minute structure of the woody walls are of primary importance.

That the initial stages of the permanent deformation have either been entirely overlooked, or that their significance has not previously been realised, may account for the diversity of the explanations of the manner of failure offered by different investigators. The grosser features of the failure of all three woods studied in detail, and of a large number of others examined more briefly, are secondary effects dependent on the anatomical structure of the particular wood. The initial failure, in all

cases, depends on primary changes, in the substance of the cell-walls, which will be described below.

### Staining Reactions in the Zone of Failure.

Before describing the more minute changes associated with the permanent deformation, reference must be made to some unexpected results which were first obtained during the preliminary study of the grosser features of the zone of failure in compressed Spruce. Similar results were later obtained for Pitch Pine, for Ash, and for a large number of other woods. It was found that the zone of failure behaved differently, towards various stains and reagents, from the uninjured parts of the wood. Plate 1, figs. 7 and 8, taken from sections through specimens of compressed Spruce, illustrate this differential behaviour of the zone of failure when the reagent used is chlor.-zinc-iodide. The zone of failure appears as a deep blue band in contrast to the yellow stain given by the unaltered wood. The blue stain is similar to that usually obtained when chlor.-zinc-iodide acts on pure cellulose. Observation, by high powers of the microscope, shows that the blueness of the zone is due to transversely running bars as seen on the surface walls of the tracheides (Plate 2, figs. 15 and 16). These blue bars are separated by narrow yellowish areas; within the actual zone of failure they are very numerous and close together, but they also are present in a more diffused manner for a considerable distance beyond the zone of failure (Plate 2, figs. 15 and 16). The blue reaction extends into the depth of the walls, and in the section of these the change is manifested by obliquely running bars of blue (Plate 2, fig. 15$x$).

An attempt was made, by using a variety of histological stains and reagents, to elucidate the nature of the change in the fractured region. Iodine and sulphuric acid give results parallel with, but even more striking, than those with chlor.-zinc-iodide. As before, the altered zone stands out in contrast to the normal parts of the wood. The deformed region gives a dark green colour rather than the blue which would have been expected if the zone consisted of pure cellulose. The rest of the wood, consisting of unaltered tracheides, gives the normal deep yellow colour. A close examination of the region of failure shows that the yellow lignin-reaction is present in the zone of failure, but that this yellow colour is largely overpowered by a blue colour in the portions which stand out blue with chlor.-zinc-iodide. The dark green stain is the result of the combination of the blue with the yellow of unchanged lignin.

Parallel results were obtained with a number of stains and reagents, and the effects of these are summarised in the following Table:—

| Stain or Reagent. | Zone of failure. | Unaltered wood. | Remarks. |
|---|---|---|---|
| Chlor.-zinc-iodide ..... | Blue | Yellow | |
| Iodine and $H_2SO_4$ ..... | Dark green | Yellow | |
| Aniline chloride ..... | Yellow | Yellow | Normal lignin-reaction throughout. |
| Phloroglucinol and HCl ..... | Pink | Pink | Normal lignin-reaction throughout. |
| Aniline chloride followed by aniline blue | Blue or bluish green | Yellow | |
| Cotton red (carthemin) followed by aniline blue | Blue | Red | |
| Safranin followed by hæmatoxylin | Blue | Red | Contrast less sharp than in other cases. |

The results obtained, using aniline chloride alone, and also those with phloroglucinol, especially point to the presence of substances giving the lignin-reaction in the zone of failure, possibly in undiminished quantity. On the other hand, the behaviour of the walls of the fractured tracheides, especially towards chlor.-zinc-iodide, iodine and sulphuric acid, and such aniline stains as aniline blue, suggests that in some way the cellulose present in the lignified walls has been unmasked as a result of the mechanical strain. This change in the staining properties of the walls of compressed tracheides has obviously a fundamental bearing on the nature of the process of lignification of the cell-wall, and it will be further discussed in this connection after the minute details of the structure of the deformed walls have been described.

Apart from slight individual differences in the staining properties of the walls of the tracheides, fibres, and vessels of different woods, it was found that, broadly speaking, the changes in the behaviour towards reagents and stains just described for Spruce held for the zone of failure in such widely different woods as Pitch Pine, Ash, Birch, Andaman Padouk, Oregon Pine, and Swamp Cypress. Whenever failure in compression occurs in wood, it is possible to demonstrate the region of failure, however slight this may be, by making use of stains and reagents. The method has been particularly useful in demonstrating the very earliest stages in the deformation of the walls of the tracheides and fibres. It has thus been possible to trace the sequence of changes in compressed specimens from the initiation of deformation up to the stage when a clear zone of failure is visible on the faces of the specimen. This sequence of changes will first be described for Spruce.

### Initial Stages of Failure in Spruce.

Test specimens were carefully compressed so that only the first signs of failure (*i.e.*, that the elastic limit had been reached and that yielding was taking place) were

evident from the behaviour of the testing machine. Sections from such specimens gave early stages in the development of the zone of failure. Plate 2, fig. 10, is the tangential view of such early stages as they appear in the relatively thin-walled spring wood. The walls of the tracheides are locally crinkled; and the crinkling extends in an approximately horizontal direction across the specimen from tracheide to tracheide. In the autumn wood, the walls of the tracheides buckle more gradually than the thinner walls of the spring wood, and are not thrown into abrupt folds like the latter.

Corresponding radial sections show the walls of the tracheides of the spring wood crinkled as in the tangential sections, and, as before, the series of local crinklings forms a horizontal band across the spring wood (Plate 2, fig. 11). The thicker walls of the tracheides of the late wood buckle gradually, and the line of the failure is usually inclined at about 45° to the length of the tracheides (Plate 1, fig. 6). Both in the tracheides of the autumn wood and in those of the spring wood, the pairs of walls of adjoining tracheides appear to behave as one, since they invariably buckle or crinkle, as the case may be, in the same direction. The ratios of the thickness of the cell-walls to the diameter of the cavities probably determines whether the crinkling seen in the spring wood, or the simple buckling seen in the autumn wood, will occur. In the passage from the spring wood to the autumn wood of the same year, the change in the thickness of the walls is a gradual one, and, in consequence, the transition from crinkling to buckling is also gradual.

The medullary rays in Spruce crinkle or buckle with the tracheides, but do not appear to form special places of weakness in the wood (Plate 2, fig. 10, *m.r.*). No separation between the tracheides and the medullary rays has ever been observed in Spruce.

The first lines of failure may pass through bordered pits as the former extend across the specimen, but no evidence was obtained that the pits form special places of weakness in the wood. Many very early stages in the failure were obtained, however, which prove conclusively that the yielding in the substance of the walls takes place, apart altogether from the presence or absence of pits. In Spruce, if the bordered pits formed special places of weakness in the woody walls, we should expect the radial walls, on which the bordered pits mostly occur, to be weaker than the tangential walls. The displacement of the elements of the wood should, on this supposition, take place in the tangential direction. It has, however, been shown above that this is not the case in Spruce, and it will be shown below that the fundamental changes that accompany the deformation of the cell-walls are not connected with the presence or with the distribution of pits. In this respect the present work is not in agreement with the conclusions of JACCARD, or with the statements of RECORD regarding the weakening effect of the pits.

### Minuter Changes preceding Buckling and Crinkling.

The buckling and the crinkling of the walls of the tracheides of the autumn and spring wood respectively are preceded by local changes in the substance of the cell-walls. These changes can readily be observed in the radial and tangential sections of Spruce wood, showing initial failures. Somewhat thick radial longitudinal sections of Spruce show the thickness of the tangential walls of the tracheides in section and the radial walls in surface view. The changes which lead to deformation consist in the appearance of extremely fine, but sharply defined, crack-like lines in the walls of the tracheides.* In the sectional views both of the radial and tangential walls of autumn and spring wood, the lines are somewhat irregularly cross-hatched, and run obliquely through the secondary layers of the walls at inclinations greater than 45° to the edge of the wall (Plate 3, figs. 1, 2, and 4; Plate 2, figs. 17 and 18). It is clear, that where each line comes out to the surface, there is a step-like projection of the wall-substance (Plate 3, figs. 1 and 2). In most cases, the direction of the lines is common to the secondary layers of pairs of walls of adjoining tracheides, but no line has been observed crossing the middle lamella between adjoining tracheides. This probably signifies a difference in the elastic properties of the middle lamella (Plate 2, fig. 17, *ml.*).

In the surface view of the walls of the spring wood, corresponding to the sectional views just described, the lines run across the walls in an approximately horizontal or transverse direction (Plate 3, figs. 1 and 4). On the surface of the walls of the autumn wood they may be either transverse, or more or less inclined to the axis of the cell, often forming a system of fine cross hatchings (Plate 3, fig. 6). The inclination of the lines, as seen on the surface of the walls, is never the same as that of the slits of the pits on the walls of the tracheides. The appearances of the lines, in the sectional views of the cell-walls and also in the surface view of these, are consistent with an explanation which regards them as the traces of planes of displacement in the cell-wall substance. The boundaries between the step-like projections, seen in the sectional views, manifest themselves as one or more series of parallel, transverse or inclined lines on the surface of the walls (Plate 3, figs. 6 and 7).

When deformation begins in the cell-walls of the wood, parts of the substance of the walls are pushed over other parts so that regular planes of slipping are locally developed. That the lines which represent the boundaries between these planes of

* It has been found that the mere mechanical effect of cutting sections, however good the knife may be, is sufficient to produce artificially a small number of these lines of slip, but tracing the appearances back from advanced to more initial failures leaves no doubt that the lines described are a direct result of the compression. In a number of instances sections were alternately cut from control uninjured specimens of wood and from the compressed specimens. The comparison of these afforded additional evidence of correctness of the interpretations given. Tracheides, isolated by maceration from a zone of failure, with practically no mechanical manipulation, show slip-lines in very large numbers in the buckled or crinkled walls, and only a few elsewhere.

slipping are sometimes inclined approximately at 45° to the axis of the cell, indicates that they are probably planes of shearing in the substance of the walls.

As the failure proceeds, the number of shearing or slipping planes rapidly increases, with the result that an extended region of the wall is affected, until finally the wall buckles or is thrown into a series of crinkles (Plate 3, figs. 3, 4, and 5). The walls, under the stress of end-compression, thus exhibit plasticity by the development of planes of slip or shear within their substance. It is by this microscopic, plastic deformation of the substance of the cell-walls that the failure is initiated. Whether buckling or crinkling subsequently occurs is determined by the relative thickness of the walls of the tracheides (Plate 3, figs. 3 and 5).

Very large numbers of early stages were observed in which slip-planes had developed before any visible buckling or crinkling had begun to take place (Plate 2, fig. 17 ; Plate 3, fig. 1). There is, therefore, no doubt that the primary mode of failure, or permanent deformation, is by the development of the microscopic planes of shear in the substance of the cell-walls. The buckling and the crinkling are subsequent developments.

After buckling and crinkling have taken place, the further development of the failure is then determined by the anatomical structure of the wood. In Spruce, as has already been pointed out, the relatively small proportion of autumn wood is probably one of the main factors in determining the ultimate and grosser characters of the failure.

The "slip-lines" or planes described here for the wood of Spruce present certain similarities to the slip-bands or gliding planes described by Ewing and Rosenhain* for the crystals of metals under strain, and by Reusch† and others at an earlier period for many crystalline substances. Since wood cannot be regarded as crystalline in the ordinary sense, the relationship between the phenomena in wood, on the one hand, and in the metals and crystals on the other, will be discussed below.

By careful illumination it is possible to observe the slip-lines described above, in unstained sections merely mounted in water. A more vivid demonstration of them, however, is obtained by staining compressed specimens with aniline chloride followed by aniline blue. These stains afford a means of demonstrating the lines even in the most initial stages of failure, before any buckling or crinkling has taken place, and before a zone of failure has developed. The lines and the wall-substance in their immediate vicinity hold the blue stain, whilst the rest of the wall remains yellow. Corresponding results are obtained with cotton red and aniline blue, and with chlor.-zinc-iodide solution. It has in fact been established that the remarkable differential staining of the zone of failure described above (pp. 54 and 55) is almost entirely due to the multiplicity of slip-planes in the substance of the cell-walls. The substance of

* Ewing and Rosenhain, 'Phil. Trans.,' A, vol. 193 (1900); Rosenhain, 'Introduction to Physical Metallurgy,' 1914.

† Reusch, quoted in Lehman's 'Molekularphysik,' vol. 1, p. 64 *et seq.* (1888).

the walls in the immediate vicinity of these microscopic slipping planes holds the cellulose stains and reagents selectively.

The staining effect is thus clearly connected with the displacement of the particles of the cell-walls in the vicinity of the slip-planes and strongly suggests the possibility of a local chemical alteration of the lignified wall at these places. On the other hand, the modification in the staining properties may merely be the result of a physical alteration in the wall-substance. It is possible that the alteration is due to an actual transformation of the lignified wall into cellulose, in the immediate vicinity of the planes of slipping. It must be pointed out that many of the staining effects obtained with ordinary dyes on cell-walls, as well as the usual reactions for cellulose, can be explained as adsorption effects. BARGER* and his collaborators, for example, have shown that iodine forms blue adsorption compounds, with a large variety of organic chemical compounds in addition to that formed by the action on starch. He has also shown that the ability of an organic substance to form such blue adsorption compounds depends on the particles of the substance being in the colloidal state. The blue colour produced in the chlor.-zinc-iodide reaction for cellulose is probably due to the formation of such an adsorption compound with iodine in the presence of zinc chloride. Lignified cell-walls normally give no such blue compound with iodine in the presence of zinc chloride.

Botanists, since the time of NÄGELI, have regarded the lignification of the cell-wall as due to the passage of incrusting substances into the substance of the cellulose wall. Expressing this view of the nature of lignification in terms of the more modern conceptions of colloid chemistry and physics, the incrusting process would consist in the adsorption of lignone substances by the colloidal particles of cellulose in the wall. The formation of such adsorption compounds would lead to the complete obscuring of each particle of cellulose by a film of lignone substances. Such a compound would, therefore, be incapable of forming blue adsorption compounds with iodine.

It is possible to think of such adsorption compounds of cellulose with lignone substances in the cell-walls of wood, as being split up by mechanical stress and the cellulose being revealed as a consequence. Such a view would explain why, even in the region of failure, the ordinary lignin-reactions can be obtained as readily as in the normal wood, but side by side with a strong cellulose-reaction. According to this explanation the mechanical strain does not result in the destruction of the incrusting substances, but merely in their ultramicroscopic rearrangement in relation to the cellulose particles by which they can be regarded as being adsorbed in the unaltered lignified walls.

* BARGER, C., and FIELD, 'Journ. Chem. Soc. Trans.,' 1912, p. 1394; BARGER, G., and STARLING, W., 'Journ. Chem. Soc. Proc.,' 1913, p. 128.

### Behaviour of Compressed Wood Towards Polarised Light.

The facts regarding the nature of the deformations in the cell-walls of compressed specimens and the interpretations which have been outlined above, received striking confirmation by the use of the polariscope. It was found that the optical properties of the walls of the deformed tracheides had been altered in important respects.

Under low powers of the microscope, with crossed nicols, the zone of failure, both in radial and tangential sections, stands out as a very bright band across the unaltered parts of the section. The band corresponds exactly in form to similar bands brought out by staining methods in other specimens. On rotating the analyser to the parallel position, the illumination of the band reverses and stands out as a dark zone crossing a brightly illuminated section. Comparison with the behaviour of the uninjured parts of the wood shows that in addition to the illumination being reversed in the zone of failure, the degree of illumination is brighter than in the unaltered parts of the wood at their brightest.

The effect under polarised light is partly due to the folding of the cell-walls and consequent altered orientation of these, but examination of walls showing slip-lines without buckling or crinkling, shows that the folding is not the main cause of the altered anisotropy in the zone of failure. Under high magnifications the coarser slip lines are particularly well demonstrated and the parts of the wall substance in the immediate vicinity of the lines show greater anisotropy than the rest of the wall. This results in the lines standing out under crossed nicols as bright lines (often red) across the darker wall, and as dark lines in the parallel position.

The polariscope thus affords an even more effective means of demonstrating the slip-lines than when staining methods are used. Both methods give clear results for Spruce, to which the above descriptions apply, but, in some other woods like Ash the shearing lines are not so easily demonstrated by the methods of differential staining, owing to the unaltered walls taking up, to some extent, the cellulose stains and reagents. In such cases the polariscope has been particularly useful as a rapid and vivid means of demonstrating the existence of lines of slip.

### Slip-Planes in Ash.

In Ash the gross characteristics of the failure, briefly referred to in an earlier paragraph, are preceded by changes in the walls of the fibres which comprise the main mechanical elements of the wood. It has been pointed out that the fibres buckle gradually under compression and finally there is a separation of the tissues at the medullary rays. The buckling of the fibres is, however, invariably preceded by the initiation of microscopic planes of slipping in the substance of the cell-walls.

The multiplication of these slip-planes leads to the buckling of the fibres as in the autumn tracheides of Spruce (Plate 3, fig. 9). The slip-lines, in the sectional views of the walls, are often inclined at an angle of about 45° to the long axis of the fibre,

but the angle, as in Spruce, may be considerably higher than this. Seen in the surface view of the walls the lines may cross transversely but are often inclined at a high angle to the longitudinal axis of the fibre; this inclination, however, is never that of the slits of the pits.

The first sign of failure, as in Spruce, is the development of these planes of shear in the cell-walls; as they increase in number and more fibres become involved the failure gradually passes over into buckling of the fibres to be followed by separation at the medullary rays. The whole process in Ash, however, is much more gradual than in Spruce, and a much greater area of fibres shows slip-lines before the buckling begins. This may be correlated with the greater plasticity of the wood of Ash than that of Spruce. Even in the autumn wood of Spruce the buckling is much sharper than is usual in Ash (Plate 1, *cf.* figs. 5 and 6).

### Slip-Planes in Pitch Pine.

In Pitch Pine the thin-walled cells of the spring wood are crinkled under compression, while the thick-walled tracheides of the late wood buckle like those of the autumn wood of Spruce. The crinkling or buckling of the tracheides in this wood is also preceded by the development of definite shearing planes in the substance of the cell-walls. These are particularly well demonstrated both by the method of differential staining and by the polariscope. The sequence of changes, leading to buckling or crinkling, is similar to that described for Spruce and for Ash (Plate 3, fig. 8). The much greater proportion of thick-walled tracheides probably largely determines the grosser characters of the failure already described.

For the three woods studied in detail, it is thus clear that the first stage in the failure under compression is the development of planes of shearing in the substance of the walls of the cells comprising the wood. The buckling or crinkling are secondary effects, depending probably on the thickness of the cell-walls. The still grosser appearances of the failures can be explained by such anatomical characters as the proportion of autumn to spring wood, and the size, nature, and distribution of the medullary rays. The main contribution of this paper, however, is the tracing of the original causes of failure back to the minute microscopic deformation of the substance of the cell-walls of wood, along planes more or less definitely orientated in relation to the direction of the stress. The general conclusions regarding the origin of failure in compression derived from the detailed study of Spruce, Pitch Pine, and Ash, have been extended to all the woods so far examined. These include Oregon Pine, Oak, Swamp Cypress, Birch, Larch, and Andaman Padouk.

### The Effect on Compression Failures of Soaking Timber in Water.

In the work described above, the moisture-content of the test specimens was that of ordinary air-dried wood, *i.e.*, from 12 to 15 per cent. of the dry weight of the

wood. It was found in a previous investigation that the compressive strength of Spruce is strikingly affected by the moisture-content of the specimen tested. For example, wood, which in the fibre-saturated condition (*i.e.*, about 30 per cent. moisture) yielded under a compressive stress of about 3000 lbs. per square inch, required about 8500 lbs. per square inch to produce failure when the moisture-content was reduced to 3 per cent. of the dry weight of the wood. It was of interest, therefore, to ascertain if this remarkable difference in the strength values at different conditions of moisture-content could be correlated in any way with differences in the microscopic characters of the strains. Some results from this point of view were obtained with specimens of Spruce soaked in water, to ensure complete fibre-saturation.

The soaked specimens were compressed in the testing machine until the indicator showed yielding had begun to take place. Sections from such specimens demonstrated that failure is initiated, as in air-dry wood, by the development of planes of slipping in the cell-walls. These slip-planes, however, are more diffused through the specimen than when dry wood is compressed. The zone of failure, which ultimately appears, is in consequence broader, and its limits are less sharply defined than before. All the appearances obtained in such soaked specimens suggest that the buckling and even the crinkling of the tracheides occur much more gradually since they are preceded by much more generalised slipping than when the Spruce is dry.

In Ash, the effect of soaking in water is even more striking than in Spruce. As before, the failure is initiated by the development of planes of slipping in the fibre walls. The initial failures so produced, however, occur in large numbers, evenly distributed through the length of the test-specimen (text-fig. 2). In Ash of ordinary moisture-content, *e.g.*, 15 per cent., the few initial failures which arise are confined to a middle region of the specimen, and lead to a zone of failure and displacement in this region (text-fig. 1). The form of the individual initial failures both in dry and in soaked Ash is the same, even though the number and distribution of these initial failures is so different.

The effect of soaking the wood of Ash and of Spruce in water is to lower considerably the value of the compressive strength of the wood, and to make it more plastic. This increased plasticity is manifested by the more ready occurrence of slipping in the substance of the cell-walls, and also by the more generalised distribution of the slip-lines in the test-specimen after failure.

In the employment of wood for certain purposes, the pieces are often shaped by bending, after soaking in warm water or steaming. The pieces are held in the bent position, and, on cooling and drying, retain the deformation given to them. This method is frequently employed in the case of Ash. It was therefore of interest to examine the microscopical effect of producing such permanent deformation by bending wood after soaking in warm water or steaming it.

Specimens of Spruce and of Ash, measuring 10 inches by ¼ inch by ¼ inch, were bent to various degrees, and held in the bent position until cold and dry. Sections through the middle of such bowed specimens showed that the permanent deformation had invariably been produced by the development of planes of slipping in the walls of the tracheides or fibres on the compression side of the specimen. These planes of slipping were regularly distributed through the deformed portion, being most abundant at the region of greatest deformation. In cases where extreme bending of the specimen was carried out, initial failures and buckling of the fibres and tracheides took place. Even where only the very slightest permanent bowing was produced, it was possible to demonstrate planes of slipping in the cell-walls in the middle part of the specimen. The facts for Ash and for Spruce, permanently deformed after soaking in warm water or steaming, are thus in entire agreement with those obtained in the compression failures of these woods in the air-dried condition.

### Fractures in Longitudinal Tension.

The gross features of the tension fractures of a number of woods, including Oak and Ash, have been described and figured by Fulton (*loc. cit.*). He found that the slipping,* which resulted in fracture, invariably occurred along the planes of the medullary rays, so that the fracture had an irregular splintery character, as seen on the tangential face, and was manifested on the radial face, as a straight break across the specimen. The results obtained for the tension fractures of Spruce, Ash, and Pitch Pine, in the present work, are not in agreement with those of Fulton, even for the gross form of the fractures. As in the failures in compression, the initiation of the fracture has been traced back to the behaviour of the substance of the walls of the individual tracheides or fibres of the wood.

The fractured specimens, which were supplied me by Major Robertson, R.A.F., were cylindrical in form with expanded ends, the central portion of the specimen being much narrower in diameter than the ends which had been held in the grips of the machine.

The gross features of the fractures may be briefly summarised. In Spruce, the fracture is normally of a splintery character, as seen both from the radial and the tangential faces, but the planes of slipping for the main splinters are generally parallel to the annual rings, and the gross slip often takes place in the spring wood in the near vicinity of these rings (text-fig. 3). A certain amount of slipping also occurs in planes at right angles to the annual rings, and this explains the splintery character, as seen in the tangential view of the fractured specimen (text-fig. 3). The history of the development of the broad picture of the fracture is probably as follows. The initial effect of the tension stress is to cause local isolated ruptures in the specimen; these ruptures result in the production of longitudinal shearing

* The slipping referred to by Fulton is a gross slipping of the tissues of the wood and not the more microscopic slipping in the substance of the walls, described in this paper.

stresses, and the rest of the material fails by longitudinal shearing. The microscopic characters of the fractured surfaces, *e.g.*, at S (text-fig. 3), are identical with those obtained in specimens of Spruce fractured by longitudinal shearing, and are therefore consistent with the explanation given.* The microscopic characters of the initial local ruptures will be described below.

In Ash the fracture is more abrupt than in Spruce, but the gross slipping in this wood also takes place along planes parallel to the annual rings, particularly in the spring wood (text-fig. 4). As in Spruce, there is also some slip in the tangential planes, but this is not so obvious in the specimens I have examined as that in the planes parallel to the annual rings. Plate 4, fig. 15, shows that the form of the fracture is not affected by the medullary rays.

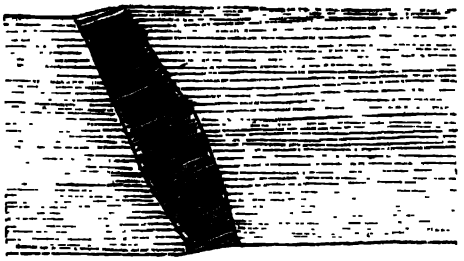
In Pitch Pine the tension fracture is usually extremely short and is transverse in character, but even here the bigger irregularities follow the planes of the annual rings rather than those of the medullary rays (text-fig. 5). Owing, however, to the normally brittle character of Pitch Pine, it is not so suitable for the consideration of the questions under discussion.

The more microscopic characters of the fractures produced by longitudinal tension may now be described. In tangential sections of the fractures of Spruce, Ash, and Pitch Pine, there is no evidence that the medullary rays form special places of weakness for pure tension stresses in the longitudinal direction. The medullary rays are so abundant that it seems unlikely that fractures could occur without involving some of them; but the specimens examined conclusively showed that the initiation of slipping could not in any way be specially related to the rays (Plate 4, fig. 18).

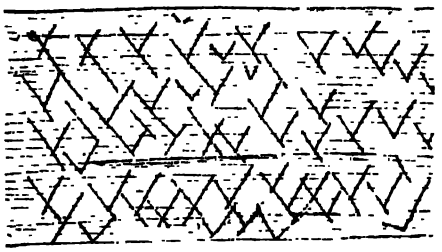
Normal specimens of Spruce in the air-dried condition give breaks of the tracheides similar to those shown in Plate 3, figs. 10 and 11. The walls of the tracheides, both of the autumn and spring wood, are ruptured along planes which have exactly the inclination of the slits of the pits. Plate 3, fig. 11, shows a complete fracture in a spring tracheide while at (S.) slipping, which has not yet led to actual rupture, is taking place. The planes of slipping in the walls and also the ruptures in these are confined to the vicinity of the pits, although the inclination of the slip-planes is the same as that of the slits of the latter. In tension failures, unlike compression failures, the initial rupture rapidly follows upon the development of planes of slipping in the substance of the walls; rupture is, therefore, preceded by the appearance of relatively few slip-lines. It is noteworthy, however, that the fractured ends of the tracheides, as well as the few slip-lines that appear, behave selectively towards stains and reagents just as do the slip-lines in the compression failures.

The slip-lines in the sectional view are generally obliquely inclined to the edge of the walls. From the general microscopic appearance of the fractured tracheides, however, there is no doubt that most of the slipping takes place in tangential planes (*i.e.*, at right angles to the surface) in the walls. Text-fig. 6 illustrates the direction

* See pp. 67–69 below.



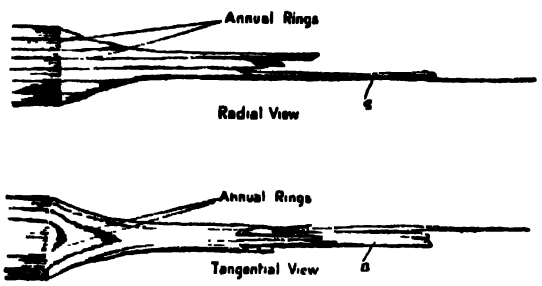
TEXT-FIG. 1.



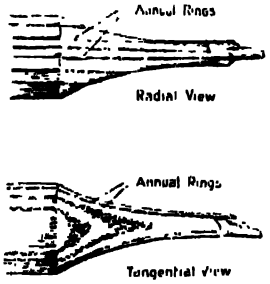
TEXT-FIG. 2.

TEXT-FIG. 1.—Diagram of zone of failure in air-dry Ash (15 per cent. moisture). × 4.

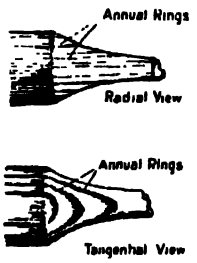
TEXT-FIG. 2.—Diagram of lines of failure in similar piece of Ash to that in fig. 1, after soaking in water. × 4.




TEXT-FIG. 3.




TEXT-FIG. 4.

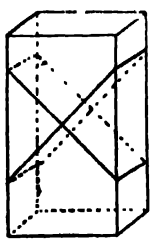



TEXT-FIG. 5.

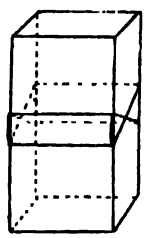
TEXT-FIG. 3.—Specimen of Spruce fractured in tension, showing appearance of fracture from the radial and tangential views. (Half actual size.)

TEXT-FIG. 4.—Similar specimen of Ash to that in text-fig. 1, fractured in tension. (Half actual size.)

TEXT-FIG. 5.—Similar specimen of Pitch Pine, fractured in tension. (Half actual size.)



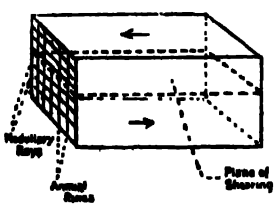
TEXT-FIG. 6.



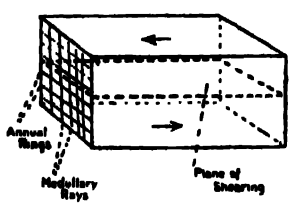
TEXT-FIG. 7.

TEXT-FIG. 6.—Diagram illustrating planes of shear in the cell-walls in tension specimens of Spruce.

TEXT-FIG. 7.—Diagram illustrating the direction of the planes of shear in the cell-walls of compression specimens of Spruce.




TEXT-FIG. 8.




TEXT-FIG. 9.

TEXT-FIG. 8.—Diagram to illustrate the direction of longitudinal shearing along a radial plane.

TEXT-FIG. 9.—Diagram to illustrate direction of longitudinal shearing along a tangential plane.

of the planes of slipping in such cases. This differs from the slipping in the radial direction in the walls (*i.e.*, parallel to the surface), which is most frequently observed in the compression failures of Spruce (text-fig. 7). In tension fractures the displacement of the wall-substance is thus in the tangential direction in the individual walls, whilst in compression failures the movement is usually in the radial direction.

For normal Spruce the substance of the cell-walls behaves differently towards tension and compressive stresses. In both cases the failure occurs by shearing in the wall-substance, but this is much less plastic in tension than in compression, since, in the former case, very few planes of slipping arise before rupture occurs. While in tension the special planes of weakness generally have the same inclination as the slits of the pits, in compression, slipping never occurs along these planes, but along planes orientated at right angles to them (*cf.* Plate 3, figs. 10 and 6).

Striking deviations from the form of tension fracture just described, were obtained for brittle samples of Spruce and also for the normal tension fracture of a number of the harder woods. In these cases the lines of fracture do not follow the inclination of the slits of the pits, but, on the contrary, the walls are broken across transversely, *i.e.*, at right angles or at a high angle to the long axis of the tracheide or fibre (Plate 4, figs. 13, 14, and 17). In the portion of the wall seen in section, it is clear that the break occurs along radial planes in the individual cell-wall, inclined at 45° or rather more to the long axis of the cell. This tension fracture of brittle wood thus occurs along planes of slipping, similarly orientated to those already described for compression specimens. Some early stages in such tension failures of a brittle sample of Spruce were obtained, and these indicated that even in this case the actual rupture was preceded by the formation of a very small number of planes of slipping in the walls of the tracheides. These planes of slipping rapidly connected up across the specimen, which then fractured (Plate 4, figs. 13 and 14).

The results obtained from tension fractures of brittle Spruce appear to indicate that the brittle qualities are associated with a greater resistance to slip along tangential planes, having the same inclination as the slits of the pits, than along radial planes in the individual walls. In normal Spruce, on the other hand, there is more resistance to slipping on radial planes than on tangential planes in the individual walls; this leads to the more splintery appearance of the fractured ends of the cells (*cf.* Plate 3, fig. 10, and Plate 4, fig. 14).

In Ash, the fibres are roughly circular in transverse section, and not, as in the tracheides of Spruce, rectangular in section. The slipping which takes place in the walls as a result of tension, occurs along oblique planes which seldom have the same inclination as the slits of the pits (Plate 4, fig. 15). As in Spruce, the tension failure occurs by slipping in the substance of the walls of the fibres, and rupture takes place before very many planes of slipping have developed. Some slight indications were obtained that more slip-planes appear in Ash before rupture than in Spruce, but it would not at present be safe to draw conclusions from this.

In Pitch Pine, the fractured tracheides present very close similarities to those seen in the brittle specimens of Spruce. The abrupt break shown in text-fig. 5 is accompanied by transverse breaks as seen on the surface of the walls of the tracheides (Plate 4, fig. 16). In this case, also, the sectional view of the walls shows slip-lines inclined at about 45° to the edge of the wall. The failure, therefore, occurs by slipping along radial planes in the substance of the cell-walls, but extremely few slip-planes are developed in any one tracheide, prior to rupture taking place (Plate 4, fig. 16).

The facts for the tension failures of Spruce, Ash, and Pitch Pine are in harmony with those already described for the compression failures of these woods. Failure takes place, both in tension and compression, by the development of planes of slipping or shearing in the substance of the cell-walls. In tension failures of brittle samples of Spruce, of normal Pitch Pine and generally of normal Ash, the planes of slip are identical with those obtained in compression. In normal Spruce and occasionally in Ash, the planes of shearing for tension failures have the same inclination as the slits of the pits. Most of the examples of failure in tension studied have shown only a very localised distribution of slip-lines in the vicinity of the fracture.

### Longitudinal Shearing.

The behaviour of wood subjected to longitudinal shearing can be correlated with the behaviour in longitudinal tension. Specimens of Spruce were fractured by longitudinal shearing both in the tangential and in the radial directions. Small rectangular pieces measuring about $\frac{1}{2}$ inch long by $\frac{1}{4}$ inch by $\frac{1}{4}$ inch were broken by pushing one part of the specimen over the other by striking a blow on the specimen held firmly in a vice. The fractures obtained by this simple method corresponded exactly in their gross and microscopic characters to those exhibited by larger specimens tested in longitudinal shearing by Major Robertson, R.A.F. It was found advantageous to use this simple method of applying the stress, since it was then possible to make microscopical observations on a large number of specimens. It was also possible to trace earlier stages in the failure than could possibly have been obtained in specimens from a testing machine.

Text-figs. 8 and 9 illustrate the directions in which the specimens were cut, and the arrows indicate the direction of the shearing. When Spruce is subjected to shearing along a tangential plane the failure always occurs in the spring wood and at rupture the fractured surfaces are finely hairy. Microscopical examination shows that the fracture occurs in the substance of the cell-walls of the tracheides and not by a separation of the tracheides from one another. Radial longitudinal sections through the fracture show that the substance of the cell-walls has been torn into a series of oblique shreds (Plate 2, fig. 12); these shreds give rise to the hairy appearance mentioned above.

The shearing stress in the tangential plane has resulted in the separation of the substance of the walls along planes which are usually inclined at an acute angle to the

long axis of the cells (Plate 2, fig. 12). Early stages in the failure are characterised by the appearance, at fairly regular intervals, of steeply-inclined, oblique splits in the walls (Plate 4, fig. 19). These splits gradually widen and as the shearing continues the tangential walls of the fractured cells become separated, the shreds produced elongating by stretching (Plate 2, fig. 12, Plate 4, fig. 19). This stretching of the shreds is accompanied by the appearance on them of fine parallel lines which are inclined to the direction of the original splits.* The shearing in the substance of the walls of the tracheides usually takes place independently of the bordered pits and is often confined to a very narrow zone of the wall near to the corner of the tracheides. The bordered pits remain intact, and instead of forming places of weakness in relation to the longitudinal shearing, appear rather to be a source of strength to the walls. It seemed possible that the shreds seen in the specimens fractured in the tangential direction might be derived in part from the tangential walls of the tracheides as well as from the radial walls shown in Plate 2, fig. 12, and Plate 4, fig. 19. Transverse sections of fractured specimens, however, proved conclusively that when the shearing takes place in the tangential plane, only the radial walls of the tracheides are shredded, and the tangential walls are not visibly affected by the stress (Plate 2, fig. 14).

When the wood of Spruce is subjected to longitudinal shearing along a radial plane (text-fig. 8), the stress operates both on the autumn and spring wood and affects each differently. In the spring wood, as before, the fracture occurs by a regular shredding of the walls along steeply inclined planes (Plate 2, fig. 13). Slight splits which are steeply inclined appear at fairly regular intervals; these gradually widen giving rise to shreds which elongate by stretching. This elongation of the shreds is accompanied, as before, by the appearance of fine parallel lines which are differently inclined from the splits (Plate 4, fig. 20).

In the autumn wood the fracture occurs by an abrupt separation of the radial walls at the middle lamella of the tracheides and at the medullary rays (Plate 4, fig. 21). There is, therefore, no shredding evident where the fracture passes through the autumn wood. The different appearances of the fracture, in the region of the autumn and spring wood respectively, are best seen in transverse sections through the fracture (Plate 4, figs. 21 and 22). The difference in the behaviour of the autumn wood is probably related to the greater thickness of the secondary layers of the cell-walls causing these to offer greater resistance to shearing than the middle lamella and the walls of the cells of the medullary rays.

The staining effect, obtained with chlor.-zinc-iodide in the case of compression failures, was also obtained in these shear failures. The shreds of the walls give the

* These fine parallel lines have all the appearances of the striations described by NÄGELI, CORRENS, etc., for the walls of fibres and other plant cells, but as is pointed out below, no such striations have ever been observed in the present work on wood, except in relation to mechanical injury and in the wood near branches.

blue colour similar to that obtained in the zone of failure in compression, and the striæ on the shreds appear as dark lines of a deeper blue colour. The mechanical stress of longitudinal shearing, therefore, produces the same sort of fundamental change in the staining properties of the cell-walls which has already been described for compression failures.

In addition to this staining effect the fractures in longitudinal shearing show features which can be further correlated with the characteristic method by which failure is initiated in compression. The longitudinal shearing stresses, operating on the wall of a tracheide (if this were isotropic), would tend to produce separation along two systems of planes inclined approximately at 45° to the direction of stress. The actual result on the thin-walled tracheides is consistent with this expectation except for the inclination of the planes. The oblique splits represent the direction of one of the series of planes of separation, while the fine striæ on the shreds are slip-lines due to the stretching. In some few instances splits occur simultaneously in both series of planes of separation giving an irregular fracture such as is seen in Plate 4, fig. 23. Much more often the splits are confined to one of the series of planes of separation and shreds are produced which show striæ or slip-lines. The anisotropy of the cell-wall probably explains the fact that the inclination of the planes of separation, as manifested by the splits and the striæ on the shreds, is not 45° to the direction of the stress.

The inclination of the planes of separation as seen on the surfaces of the walls, unlike that of the gliding planes, which have been decribed above, for compression failures, is similar to, or identical with, that of the slits of the pits. This correspondence between the inclination of the splits and that of the pit-slits, as well as the possible nature and effect of the natural anisotropy of the cell-wall will, be discussed below, in connection with the general questions bearing on the internal structure of the woody cell-walls.

## Discussion of Results and Theoretical Considerations.

The discovery that the permanent deformation of wood under mechanical stress takes place by the development of planes of slipping in the walls of the cells of which it is composed, has led to fundamental conclusions regarding the ultimate mechanical properties of wood. The properties depend primarily on the behaviour of the substance of the cell-walls, and only secondarily on the arrangement of the individual cells and tissues in the wood. In this sense wood is a mechanical structure the qualities of which depend even more on the material of construction, that is the cell-wall substance, than on the distribution of material in the structure.

The behaviour of the cell-wall substance towards mechanical stresses in the development of planes of slipping, presents striking similarities to the mechanical properties of other substances. Reusch (*loc. cit.*), in 1867, described the production of gliding planes in the crystals of many ordinary salts as a result of compression. His

observations have been extended by many other investigators, and the gliding planes are now recognised as localised planes of slipping which may form planes of cleavage for the crystals. More recently EWING and ROSENHAIN (*loc. cit.*) have shown that the plastic deformation of metals is due to the development of gliding planes within the crystals of which the metals consist. They hold that plastic deformation can only take place by gliding on the slip-planes of true crystals, and that the plasticity of metals is bound up with their crystalline structure. The slip-planes arise in directions which bear a definite relationship to the crystallographic axes, but as far as I am aware no relation has been traced between the directions of stress and those of the slip-planes in the individual crystals of the metals.

The well-known LUDER'S lines which often appear on strained specimens of certain metals have, however, according to HARTMANN* and also to GULLIVER,† inclinations which approximate to those expected of planes of maximum shearing, *i.e.*, 45° to the direction of the stress. It is also generally recognised that LUDER'S lines are outward manifestations of large numbers of the microscopic gliding planes in the crystals of the metal. The general direction of the slip follows the plane of least resistance in the substance of the metal, since it is reasonable to suppose that the minute size of the heterogeneous crystalline components allows the metal to behave as an isotropic substance.

The substance of the cell-walls of wood is probably, most correctly, regarded as of a colloidal nature, but at the same time it must be pointed out that the cell-walls show many important resemblances to crystals. These resemblances must be taken into account in the consideration of the nature of the planes of slipping which arise in wood under mechanical stress.

NÄGELI‡ was the first to attempt to relate the properties of cell-walls to conceptions of molecular physics. He studied the double refraction of cell-walls, their swelling properties and the visible microscopic structure, and was led from his observations over a wide field to propose the micellar hypothesis of the structure of cell-walls and other organised substances. According to this hypothesis the cell-wall consists of crystalline molecular aggregates or micellæ, arranged in a definite manner to build up micellar complexes. The micellar complexes are orientated in rows, and the fine spiral striations seen on the walls of many elongated cells represent alternating micellar rows having respectively greater or less water-content. The inclination of the striations, when present, is the same as the inclination of the slits of the pits, and even where striæ are not readily visible the direction of the micellar rows

* GULLIVER, "Some Phenomena of the Permanent Deformation of Metals," 'Proc. Inst. Mech. Engineers,' 1905, p. 141; 1907, p. 579.

† HARTMANN, 'Distribution des Déformations dans les Métaux, etc.,' Paris, 1876.

‡ NÄGELI, 'Bot. Mitth.,' vol. 1, "Die Anwendung des Polarisation apparates auf die Unters. des vegetabilischen Elementartheile," 1862, p. 183; 'Bot. Mitth.,' vol. 2, "Über den innern Bau der vegetabilischen Zellenmembranen," 1864, pp. 1–102; 'Theorie der Gährung,' 1879.

has been inferred by NÄGELI and later investigators from the slits of the pits. NÄGELI found that the directions of greatest swelling and of greatest optical elasticity were connected with the direction of inclination of the striæ. In the elongated cells of wood the axis of greatest swelling is in a radial direction in the wall, that is at right angles to the surface. The axis of least swelling lies in the tangential plane, that is parallel to the surface of the wall, and is inclined in the spiral course of the striæ or pit-slits. An intermediate amount of swelling takes place along a tangential axis at right angles to this. The axes of optical elasticity are the inverse of these, the least in the radial direction, the greatest along the spirals of the striæ, and the intermediate one at right angles to these.

The main trend of botanical opinion has favoured, more or less completely, the micellar hypothesis of NÄGELI; it is a remarkable tribute to the hypothesis that even quite recently some workers with colloids, such as BACHMANN,* VON WEIMARN,† and BRADFORD‡ should have made use of some of the main conceptions of NÄGELI, in explaining the structural properties of gels. It has, however, been frequently pointed out that many of the facts, on which the micellar hypothesis was based, are incorrect. These facts need not be referred to in detail, but NÄGELI's conception of essentially crystalline character of the cell-wall in plants must be considered in relation to the present work on wood. To-day, the substance of the cell-wall is usually regarded as an emulsoid gel. It is, therefore, probably non-crystalline in structure for, according to Wo. OSTWALD§ and to BACHMANN, no emulsoid gel has been proved to be crystalline. VON WEIMARN, however, regards many gels as possessing crystallinity, and BRADFORD has recently extended VON WEIMARN'S theory to certain of the organic gels. Alternative explanations to the micellar hypothesis have been proposed, but, with the possible exception of STRASBURGER'S‖ molecular-net hypothesis, none of them has attempted to explain more than one or two of the sets of properties first studied (in this connection) by NÄGELI. PFEFFER¶ has pointed out that the properties of elasticity and rigidity have not been investigated in connection with the molecular structure of organised bodies, and I am not aware of any previous work from this point of view. The bearing of the behaviour of the cell-wall substance of wood towards mechanical stress, on hypotheses of the structure of cell-walls must, therefore, be dealt with at some length.

Striations of the nature of those described by NÄGELI (*loc. cit.*), CORRENS,** DIPPEL,††

* BACHMANN, "Unters. u. die ultramikros. Struktur von Gallerten," 'Zeit. für Anorgan. Chem.,' vol. 73, p. 128 (1912).

† WEIMARN, VON, 'Koll. Zeitschr.,' vol. 4, p. 317 (1908); vol. 5, p. 62 (1909); vol. 6, p. 32 (1910).

‡ BRADFORD, S. C., 'Biochem. Jl.,' vol. 11, 1917; vol. 12, 1918; 'Science Prog.,' vol. 12, 1917.

§ OSTWALD, Wo., 'Colloid Chemistry' (Eng. Ed.), 1915, pp. 56–65, etc.

‖ STRASBURGER, 'U. d. Bau Wachstum d. Zellhäute,' 1882; 'Histologische Beiträge,' vol. 2 (1889).

¶ PFEFFER, 'Plant Physiology,' vol. 2, pp. 70–83.

** CORRENS, 'Jahrb. für Wiss. Bot.,' 1892, p. 254; 1894, p. 587.

†† DIPPEL, 'Das Mikroskop,' 1898.

KRIEG* and others have not been observed in the woods here investigated when in the uninjured condition. But this is not surprising, since the descriptions referred to are for the most part from wood obtained in the vicinity of branches or from fibres which had been subjected to chemical or mechanical treatment. In the specimens used in the present work, there was little possibility of any of the pieces consisting of wood from the neighbourhood of branches.

Although, however, striæ have not been met with, spirally inclined slits of pits have been observed continually on the walls of the tracheides and fibres (Plate 1, fig. 9). It has been mentioned above that the inclination of these slits has usually been regarded as a good indication of the direction of the micellar rows.

It has been shown in the above study of the failure in longitudinal compression of Spruce, Ash, and Pitch Pine, that the planes of slipping are always inclined differently from the planes of inclination of the slits of the pits, and generally form a high angle with them. In Spruce, for example, the slits of the pits are steeply inclined, and only form a small angle with the axis of the cell, as seen in surface view. The slip-lines run transversely across the surface of the walls of the thin-walled cells or are inclined at a high angle (more than 45°) in the thick-walled cells. In both cases the lines run obliquely in the section of the wall, but at an angle of more than 45°, to the long axis of the cell.

The displacement for compression failures is thus never along the planes of the slits of the pits, and, except for the fact that the inclination of the slip-planes to the direction of stress is always greater than 45°, the behaviour of the material of the walls is such as might be expected from an isotropic substance.

The anisotropy of the cell-walls, as regards their mechanical properties, is more striking in connection with the different behaviour in tension and compression. It is well known that the strength of wood is much greater in longitudinal tension than in end-compression. The different microscopical characters of the fractures can be correlated with this difference. It has been seen that increasing stress in end-compression leads to the development of increasing numbers of slip-planes in the substance of the walls, but that actual rupture rarely, if ever, occurs along these, failure being finally manifested by buckling and crinkling of the fibres. In tension there is a greater resistance to the development of slip-planes, and very few of these appear, but slipping along them is followed by rupture almost immediately. The microscopic facts, therefore, indicate that the gradual plastic yielding of the substance of the cell-walls, which occurs in compression, does not take place to anything like the same extent in tension. The fact that, in Spruce, after the initial ruptures have occurred in tension, the rest of the material fails by longitudinal shearing, does not affect this conclusion. If the substance of the cell-walls were isotropic, it seems

* KRIEG, 'Beihefte zum Bot. Centralb.,' vol. 21 (1907),

reasonable to suppose plastic yielding would be manifested both in tension and compression in a similar manner.

In tension the inclination of the planes of slipping differs for different woods, but two main types have been observed. These are illustrated by normal Spruce on the one hand, and by Pitch Pine, brittle specimens of Spruce, and by Ash on the other. In the first of these types the slip-planes follow the same inclination as the slits of the pits. The hypothetical micellar rows, therefore, form planes of weakness for longitudinal tension in the cell-walls of normal Spruce and Ash. In the second type* (*e.g.*, Pitch Pine, brittle Spruce, and Ash) the slip-planes are orientated in the same manner as in the compression failure, and, consequently, in these cases, the planes parallel to the slits of the pits do *not* form planes of less resistance than the rest of the wall. In the first type there seems to be less cohesion, for tension stress, between the particles of wall-substance along the planes of the slits, than in any other direction. In the second type there is no such obvious difference between the cohesion in any one direction and in any other,† and the fracture therefore approximates more closely to planes of maximum shear in the cell-walls. It is perhaps noteworthy in this connection that brittle specimens of Spruce often give strength-values in tension tests which are not so widely different from the values in compression tests as are those of normal Spruce.‡

The failure of Spruce in longitudinal shearing is initiated by the appearance of obliquely-inclined splits, on the surface of the walls, which stand at right angles to the plane of shearing. The natural anisotropy of the cell-wall causes the splits usually to follow the inclination of the slits of the pits; the shreds produced, elongate by slipping, along planes inclined to these. The slip-lines on the shreds present all the characters of the spiral striations described by NÄGELI and his followers for the walls of many elongated cells.

When longitudinal shearing stresses operate on thick-walled cells, *e.g.*, in the autumn wood of Spruce, or in the fibres of hard woods, separation occurs in the middle lamella between adjoining cells. The middle lamella offers less resistance to the shearing stresses than the other layers of the thick wall. This mechanical weakness of the middle lamella is not manifested in the tension and compression failures since the stress is mainly taken by the other layers of the wall in these cases.

It would be possible to use, to some extent, the facts described above in support of the micellar hypothesis of NÄGELI. It has been shown that, in regard to their mechanical properties, the cell-walls of wood manifest an anisotropy closely parallel to that shown in regard to such other physical properties as double refraction and swelling. In terms of the micellar hypothesis, the axes of greatest optical elasticity,

* Andaman Padouk and Swamp Cypress also conform to this type.

† The different degrees to which plastic yielding by slipping occurs in tension and compression, respectively, of course holds for both types.

‡ I am indebted to Major ROBERTSON, R.A.F., for this information.

of greatest mechanical rigidity, and of least swelling on the one hand, and the axes of greatest swelling, of least mechanical rigidity, and of least optical elasticity on the other, would be identical. This would be in general agreement with the facts derived from the microscopic appearances of the cell-walls of wood after failure in compression, in tension and in shearing in a longitudinal direction respectively. It has already been pointed out, however, that the conception of crystalline micellæ as the ultimate particles of cell-wall substance is not in accord with many modern views regarding the structure of colloid gels (p. 71). Neither is the micellar conception necessary to explain the facts described above for wood. It seems to me that a mechanical hypothesis of the structure and properties of the colloidal cell-wall explains all the known facts.

The salient points of the alternative hypothesis of cell-wall structure, which I have been led to propose from this study of the minute mechanical properties of the cell-walls of wood, will now be outlined. The cell-wall in plants has usually been regarded as a secretion product of the protoplasm. On the basis of modern views of surface energy and adsorption, it is conceivable, however, that the membrane in vegetable cells arises, first, by the accumulation of pectic substances, and then of cellulose, at the surface bounding the protoplasm. This accumulation at the surface would occur passively, as the substances arose in the protoplasm by reason of their capacity to reduce the surface energy of the protoplasm according to the GIBBS-THOMPSON law. The cellulose, thus accumulating at the protoplasmic boundaries in the growth of the membrane, will be in the condition of a highly viscous fluid, but, as the membrane grows, the viscosity increases, and finally the membrane attains the qualities of a rigid gel.

In the flow of mobile liquids, the displacements of the particles in relation to one another are uniform, in other words, such liquids under mechanical stress exhibit homogeneous shearing. EWING and ROSENHAIN (*loc. cit.*) have further pointed out that even viscous fluids may manifest homogeneous shearing. KUNDT,* however, has shown that, when even dilute sols of gum, collodium, etc., are subjected to mechanical deformation by rapidly rotating layers between two glass surfaces, a transitory double refraction is observed. The shearing produced in such cases must be heterogeneous, but, since no microscopic change is visible, an ultramicroscopic heterogeneity of shear must be thought of in this case. If, however, a membrane possessed even a small amount of rigidity, the shearing produced under mechanical deformation might be permanent, and yet ultramicroscopic, and thus only manifested by the development of double refraction. On the other hand, the permanent deformation of a more rigid membrane would give rise to a more gross heterogeneous shearing along microscopic planes of shear, the traces of which would be visible in the membrane. In other words, in the shearing of mobile, viscous, semi-viscous, and rigid substances, there must be every transition possible, from a condition

* KUNDT, 'Wied. Ann.,' vol. 3, p. 110 (1881).

of absolutely uniform or homogeneous shearing of the particles, through a permanent ultramicroscopically heterogeneous shearing, to a grosser heterogeneity of shearing in rigid substances. In such rigid substances, the individual planes of shear are separated by apparently homogeneous layers, with no visible manifestation of shearing.

From the above theoretical considerations, it follows that the anisotropy of the cell-wall can be explained as due to strains* produced by the operation of mechanical stress on the semi-rigid substance of the cell-wall in its developmental history. In other words, in the growth and solidification of the cell-wall, large numbers of minute slip-planes develop, and this causes the wall to become anisotropous. These planes are either wholly ultramicroscopic, or also microscopic in character; in the one case they are manifested only by the double refraction of the cell-wall, and in the other also by the striations and the slits of the pits. It is perhaps not without significance, in relation to this hypothesis, that the young cell-wall, *e.g.*, of cambium cells, is not doubly refractive, but only becomes so later. BUTSCHLI† has shown that it is possible, by applying tension to hardened threads of gelatine, to produce markings which present extraordinary similarity to the fine striations of bast fibres. Although BUTSCHLI did not apply a mechanical significance to these markings, which I also have observed, it seems to me there is no doubt that they represent planes of slipping in the threads. It is further noteworthy that it is quite easy to produce striations in cell-walls, artificially, by mechanical treatment, and the conclusions of NÄGELI and others are open to criticism on this account. Such artificial "striations" have been described above in connection with the failure of the wood of Spruce in longitudinal shearing. NÄGELI regarded his mechanical treatment as merely revealing the predetermined inner structure of the wall. In my view, many of the striations were created by this mechanical treatment, and really represent microscopic planes of slipping in the wall-substance.

Little is known of the forces available in the growing cells of plants to account for the permanent deformations postulated above. It is, however, well known that in the development of tracheides and fibres from cambium cells considerable extension both in length and in diameter of the cells takes place. It is true that NÄGELI and SCHWENDENER‡ have maintained that this extension takes place by growth and not merely by stretching, but STRASBURGER,§ KRABBE‖ and others have shown that plastic stretching often occurs. The mechanism by which such plastic stretching could

* The strains, thought of, are real strains in the mechanical sense, and not the internal tensions or stresses postulated by VON HOHNEL and STRASBURGER, and recently revived by HARRISON ('Roy. Soc. Proc.,' A, vol. 94, 1918) to explain the double refraction of textile fibres.

† BUTSCHLI, "Unters. über Strukturen, u.s.w.," 'Verh. Nat.-Hist. Verein Heidelberg,' vol. 4 (1896).

‡ NÄGELI and SCHWENDENER, 'Das Mikroskop,' 1877, 2nd Aufl.

§ STRASBURGER, *loc. cit.*

‖ KRABBE, "Beitrag zur Kenntnis der Struktur u. des Wachstums Veg. Zellhäute," 'Jahrb. Wiss. Bot.,' vol. 18, pp. 346–424 (1887).

take place would be the development of the ultramicroscopic or microscopic slipping conceived of above.

In the present work it has been shown that permanent deformation in the cell-walls of wood takes place by the development of planes of slipping in the substance. This conception is now being carried back to the developmental history of such cell-walls and the peculiarities of the natural walls are regarded as manifestations of mechanical forces which have operated on them during the course of their development. In this connection it is perhaps significant that in the vast majority of the cases where striations have been observed the cells have an elongated form. It is further possible that some of the mechanical forces acting on the cell-wall in the course of its development arise as the hardening membrane contracts by loss of water in its fixed position.

In wood the greater resistance to plastic deformation by slipping in tension than in compression would receive some explanation on the view that tensile strain in the previous history of the cell-walls had rendered them less susceptible to further plastic deformation in tension. It is conceivable that further slipping in tension is not possible because all the available planes of slip have been utilised for the developmental straining. ROSENHAIN (*loc. cit.*), BEILBY,* and others have described similar phenomena for metals. These often show hardening and enhanced resistance to plastic deformation in tension after having undergone tensile strain. In some such cases the strain-hardened metal is more easily deformed in compression than in tension: that is, the strain hardening is uni-directional. This mechanical anisotropy in strain-hardened metals is somewhat analogous to that seen in wood.

The analogy, with the essentially crystalline metals, must not be pressed too far for wood, which, on the the views already expressed is not truly crystalline in nature; but the resemblances may not be wholly without significance. In the case of wood it is held that the planes of slipping are not orientated in relation to any real crystallographic axes, but that they approximate to the planes of maximum shearing according to the direction of the stress. The orientation of these planes, however, is never 45°, as for isotropic substances, but is modified for particular stresses by the previous plastic deformations the wall-substance has undergone in the developmental history of the cell-walls. The above explanation of the mechanical anisotropy of the cell-walls of wood in my view, also satisfactorily explains the anisotropy in regard to their other main physical properties. The hypothesis that the mechanical anisotropy, as well as the double refraction and visible structure of the cell-walls may be explained as a result of mechanical causes operating on the substance of the cell-wall in the course of its development from a highly viscous fluid to a more rigid condition, has been framed almost solely in relation to facts derived from the study of the mechanical properties of wood. Further detailed investigation of the properties of the cell-wall

* BEILBY, 'Roy. Soc. Proc.,' A, vol. 72 (1903); vol. 76 (1905); vol. 79 (1907); vol. 82 (1909).

in plants over a wider and more varied field will show whether the hypothesis can have a more generalised application.

## Summary.

1. The initial phenomenon of the permanent deformation of wood under end-compression, longitudinal tension, and longitudinal shearing, is the development of microscopic planes of slipping in the substance of the cell-walls of the wood.

2. The gross characteristics of failure in compression are described for Spruce, Ash, and Pitch Pine. The broad results for Ash and Pitch Pine confirm those of previous investigators, but Spruce shows important differences. It is shown that the gross characters of the failure in different woods are probably determined by the anatomical structure of the wood, but that primary changes due to the development of planes of slipping in the cell-walls precede the secondary effects described by previous investigators. The microscopic planes of slipping have not previously been recognised in wood.

3. The development of the slip-planes in the cell-walls is accompanied by profound changes in the behaviour of these towards many stains and reagents. The altered parts of the cell-walls behave as if free cellulose were present there. This effect is discussed in relation to its possible bearing on the process of lignification of cell-walls.

4. The gross and microscopic features of the failure of Spruce, Ash, and Pitch Pine in longitudinal tension are described. In all cases failure is preceded by the development of slip-planes, but only relatively few of these arise, and rupture occurs along some of them much more quickly than in compression failures.

5. The failure in longitudinal shearing is described for Spruce, and it is shown that the manner of failure is to some extent affected by the relative thickness of the cell-walls under stress. Failure takes place by the development of slip-planes, if the walls are relatively thin, and by separation at the middle lamella if the walls are thicker.

6. An attempt has been made to correlate the microscopic effects of the various forms of stress with the visible structure of the cell-walls, and with the double refraction of these. It has been found that the slip-planes developed in compression failures are not inclined similarly to the planes of the slits of the pits on the cell-walls. The failure in tension of normal Spruce, and also in longitudinal shearing of the spring wood of Spruce, occurs along planes having the same inclination as the slits of the pits, and therefore the same as that of the hypothetical micellar rows of Nägeli. In many other woods, the failure in tension occurs along slip-planes similarly orientated to those obtained in compression failures.

7. The general behaviour of the cell-walls of wood is discussed in relation to the micellar hypothesis of cell-wall structure. The microscopic characters, accompanying the permanent deformation of wood by tensile and compressive stresses respectively, are different. The differences, which consist in the much smaller amount of slipping

which precedes rupture in tension than in compression in all the woods studied, and in the different inclinations of the planes of slipping in some of the woods, can be correlated with the differences in the numerical values, obtained for the strength under these stresses. It is pointed out that this mechanical anisotropy of the cell-walls is not wholly inconsistent with the micellar hypothesis of NÄGELI, which was framed to explain the anisotropy in other properties of cell-walls. Since, however, fundamental portions of NÄGELI'S hypothesis, such as the postulating of crystalline ultimate particles, are not necessary to explain the facts, an alternative hypothesis of cell-wall structure is proposed.

8. In the hypothesis, it is suggested that the mechanical anisotropy, as well as the double refraction and visible structure of cell-walls, may be explained as a result of mechanical causes operating on the substance of the cell-wall in the course of its development from a highly viscous fluid to a more rigid condition.

## DESCRIPTION OF PLATES.

### PLATE 1 (Photographs).

*s.*, spring wood; *m.r.*, medullary ray; *r.*, place of rupture; *x.*, slip lines; *a.*, autumn wood; *f.*, zone of failure; *m.l.*, middle lamella; *p.s.*, pit-slits.

Fig. 1.—Compressed piece of Spruce, showing the zone of failure as seen on the tangential face. × 5¼.

Fig. 2.—The same piece of Spruce as in fig. 1, showing the zone of failure as seen on the radial face. × 5¼.

There is marked displacement in the radial direction; the displacement is most apparent at the limits of the annual rings, *i.e.*, where the autumn wood of one year abuts on the spring wood of the next year. There is no such evident displacement on the tangential face (fig. 1).

Fig. 3.—Tangential longitudinal section of a compressed piece of Pitch pine, showing the steeply inclined zone of failure. The displacement in the tangential direction is very marked, and an incipient zone of failure is seen in addition to the main zone. × 28.

Fig. 4.—Portion of the zone of incipient failure from the same section as fig. 3, showing the separation between the tracheides and the medullary rays. × 67.

Fig. 5.—Radial longitudinal section of compressed Spruce. A portion of a zone of failure is seen, showing the crinkling and buckling of the tracheides of the spring and of the autumn wood respectively. The radial displacement is obvious, and some separation of the elements has taken place at the annual ring. × 67.

Fig. 6.—Tangential longitudinal section of a compressed piece of Ash, showing the inclined zone of failure. The displacement in the tangential direction and the separation between the fibres and the medullary rays are clearly seen. × 28.

Fig. 7.—Tangential longitudinal section passing through the zone of failure in Spruce. × 9.

This has been stained by chlor.-zinc-iodide, and the reagent has swollen the zone of failure and straightened the tracheides. It shows the remarkable alteration in the staining properties of the zone of failure.

Fig. 8.—Radial longitudinal section passing through the zone of failure in Spruce. × 9.

This section was similarly treated to that in fig. 7, and shows equally clearly the change in the staining properties of the zone of failure. The reagent has swollen the zone and straightened the tracheides so that the displacement in the radial direction is not obvious, but the staining brings out the peculiar outline of the zone of failure in relation to the annual rings.

Fig. 9.—Portion of radial longitudinal section through compressed Spruce, showing the early stages in the development of the zone of failure. The bands of failure appear light on the darker background.

The crinkling of the spring tracheides is seen and also the early stages which lead to buckling in the thicker-walled autumn wood. The inclined slits of the bordered pits are seen in the photograph. × 67.

## Plate 2 (Photographs).

Fig. 10.—Tangential longitudinal section of a compressed piece of Spruce, showing early stage in failure by crinkling of the walls of the tracheides. × 67.

Fig. 11.—Radial longitudinal section of a compressed piece of Spruce, showing slightly later stage in failure by crinkling of the walls of the tracheides. × 67.

Fig. 12.—Radial longitudinal section of a specimen of Spruce, fractured by longitudinal shear in a tangential plane. × 67.

The shearing has occurred in the walls of tracheides of the spring wood, and the wall substance has been stretched out into obliquely running shreds. (See also Plate 4, fig. 19.)

Fig. 13.—Tangential longitudinal section of a specimen of Spruce, fractured by longitudinal shear in a radial plane. The shearing has taken place in the walls of the tracheides, and the incipient production of shreds is seen. × 67.

Fig. 14.—Transverse section of similar piece, fractured by longitudinal shear in a tangential plane, to that shown in fig. 12. × 67.

The drawing out into shreds is seen to be confined to the substance of the radial walls of the tracheides.

Fig. 15.—Portion of radial longitudinal section passing through marginal portion of zone of failure in Spruce treated with chlor.-zinc-iodide. × 67.

The deep stain within the zone of failure is seen to be due to the multiplicity of bars of wall-substance which have stained selectively. These bars extend beyond the actual zone of failure, but are much less frequent, being separated by considerable zones of unaltered cell-walls.

Fig. 16.—Portion of tangential longitudinal section similar to the tangential section shown in fig. 15. × 67.

Again the presence of the deeply staining bars is seen, even outside the actual zone of failure.

Fig. 17.—Walls of tracheides of autumn wood of Spruce, in radial longitudinal section, showing commencement of permanent deformation by the development of oblique planes of slipping in the secondary layers of the wall-substance. No slip lines are evident in the middle lamella.

Photographed by polarised light with crossed nicols. × 350.

Fig. 18.—Similar photograph to fig. 17, showing the multiplication of slipping planes leading to crinkling of the cell-walls. × 350.

## Plate 3 (Drawings).

(Figs. 1 to 7 of Spruce.)

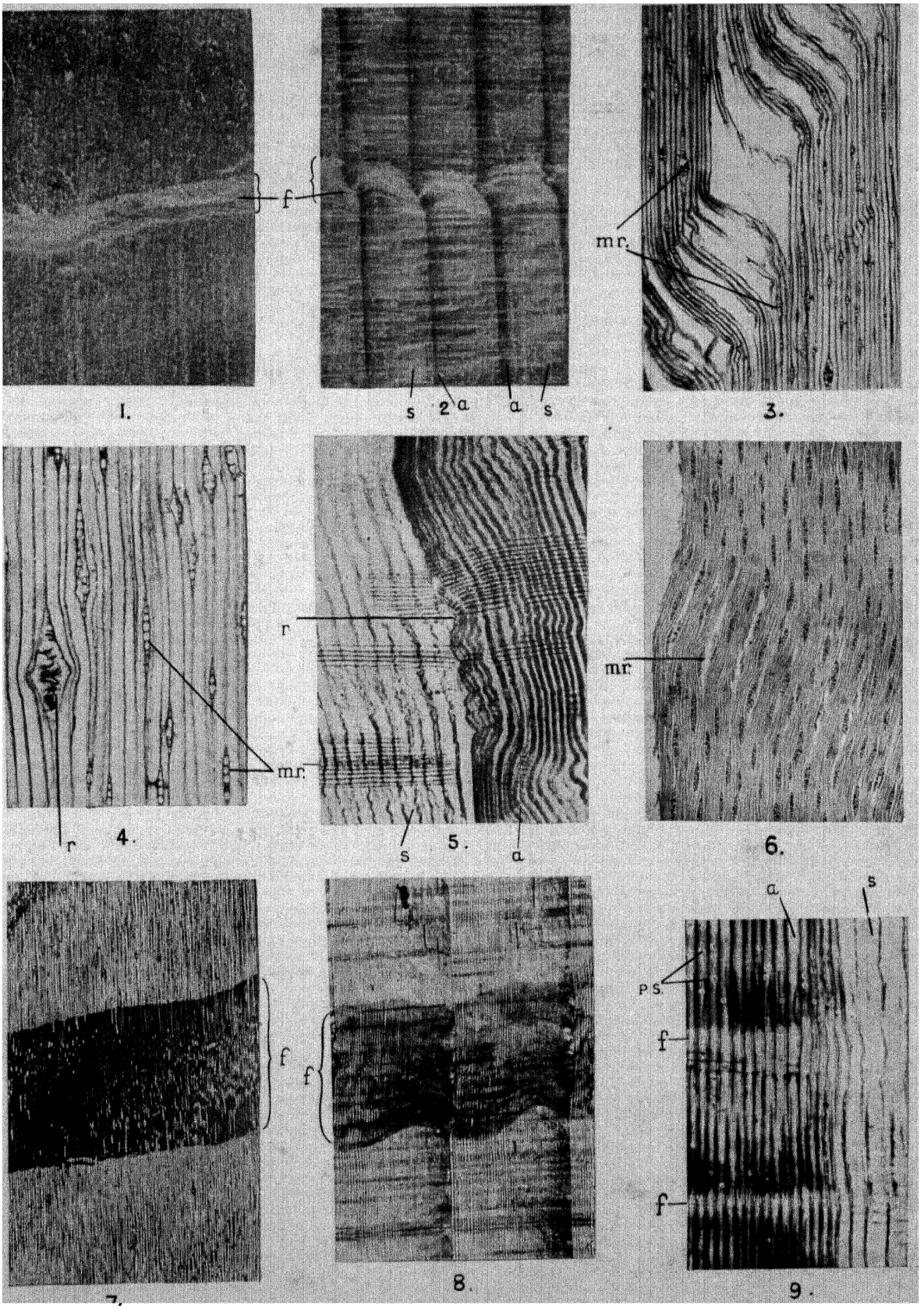
Fig. 1.—The walls of the autumn tracheides of Spruce seen in tangential longitudinal section, showing very early stages in the development of slip planes. No bending has yet occurred. × 900.

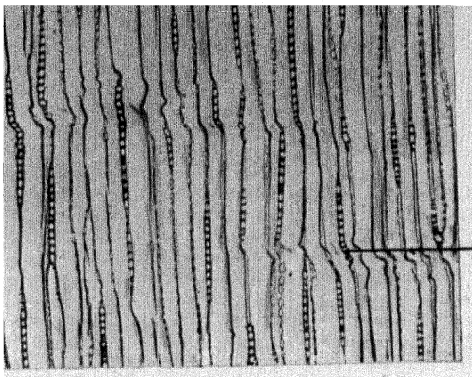
Fig. 2.—Walls of two adjoining tracheides of autumn wood similar to those in fig. 1, showing later stages in the slipping. The number of planes of slipping has greatly multiplied, and buckling is about to occur. The step-like projections of the substance of the wall are shown. × 900.

Fig. 3.—Walls of tracheides of autumn wood of Spruce, showing still later stage than in figs. 1 and 2. Buckling has now taken place as a result of the great multiplication of lines of slipping. × 600.

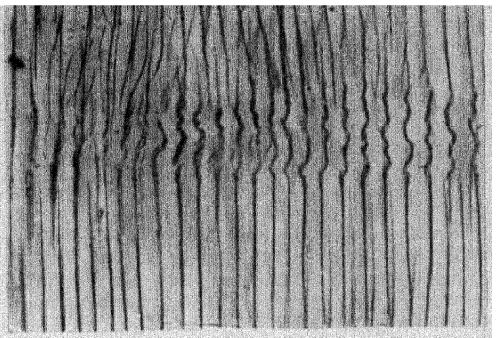
Fig. 4.—Walls of tracheides of spring wood of Spruce in radial section, showing early stage in the development of slip-planes, and in this case rapidly leading to crinkling. × 900.

Fig. 5.—Walls of tracheides of spring wood of Spruce at slightly later stage than in fig. 4, showing crinkling due to the multiplication of slipping planes. × 900. (*Cf.* Plate 2, fig. 11.)


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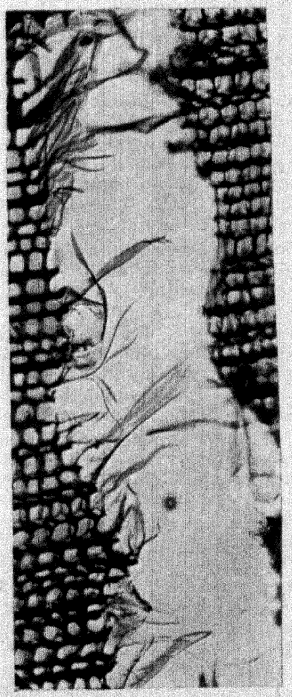
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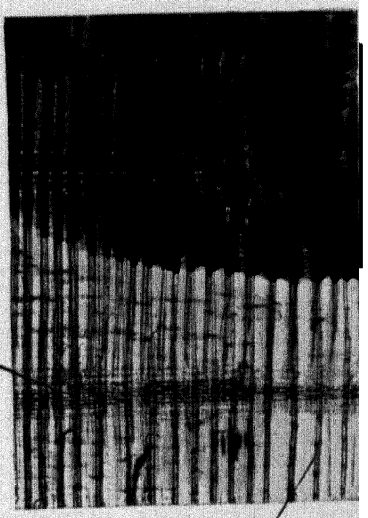
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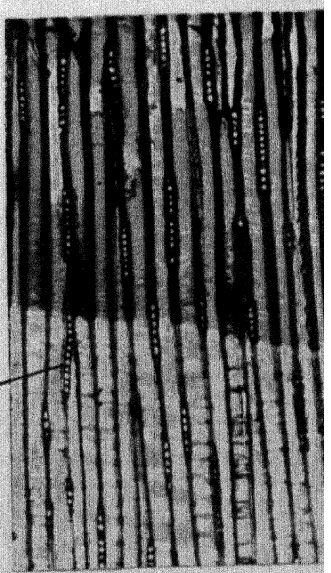
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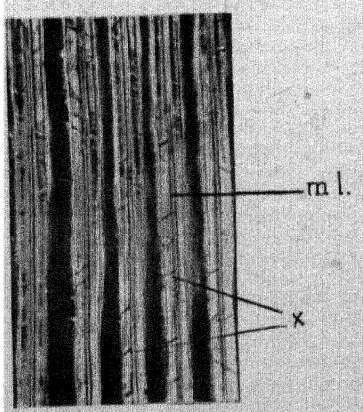
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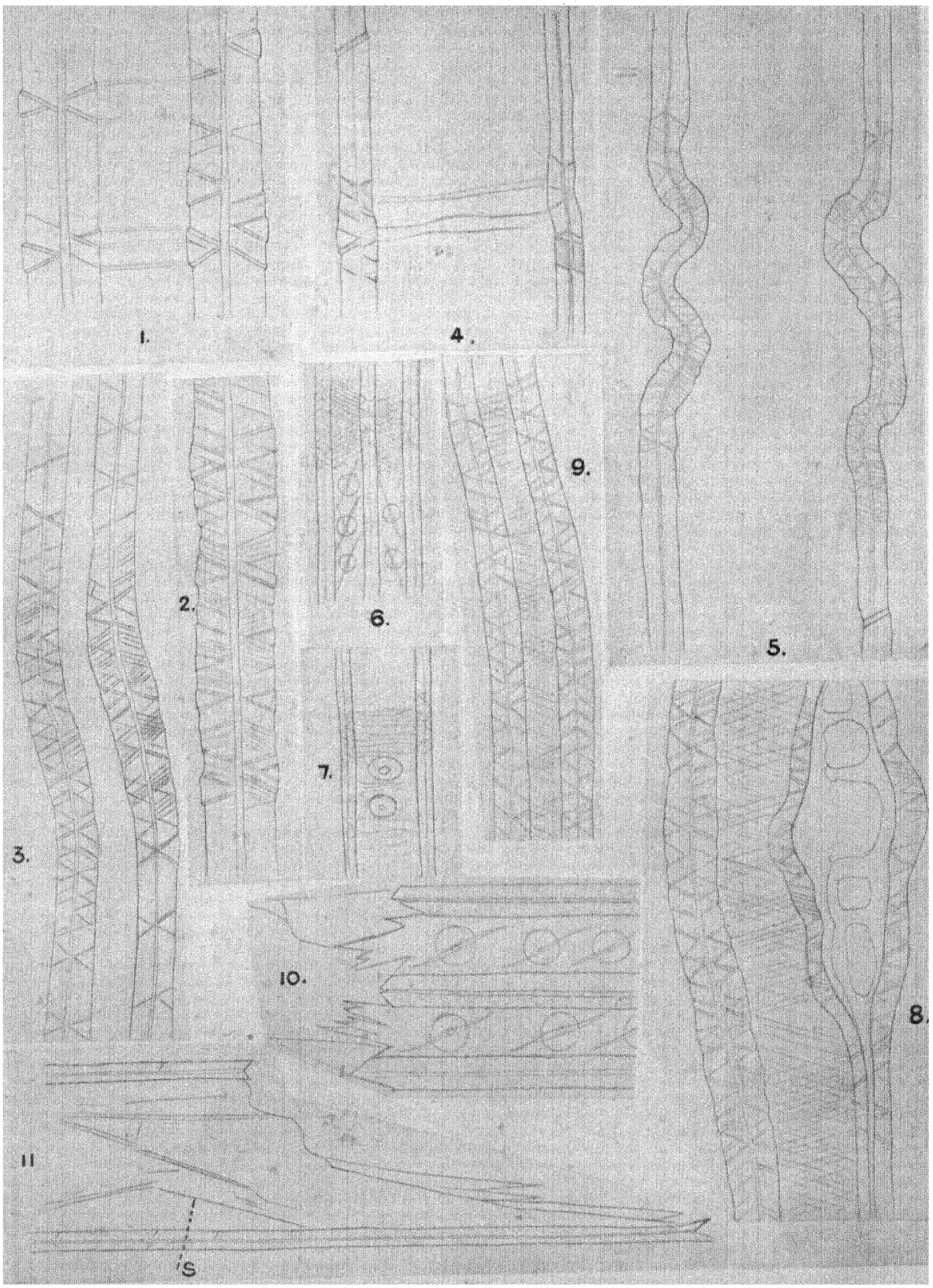

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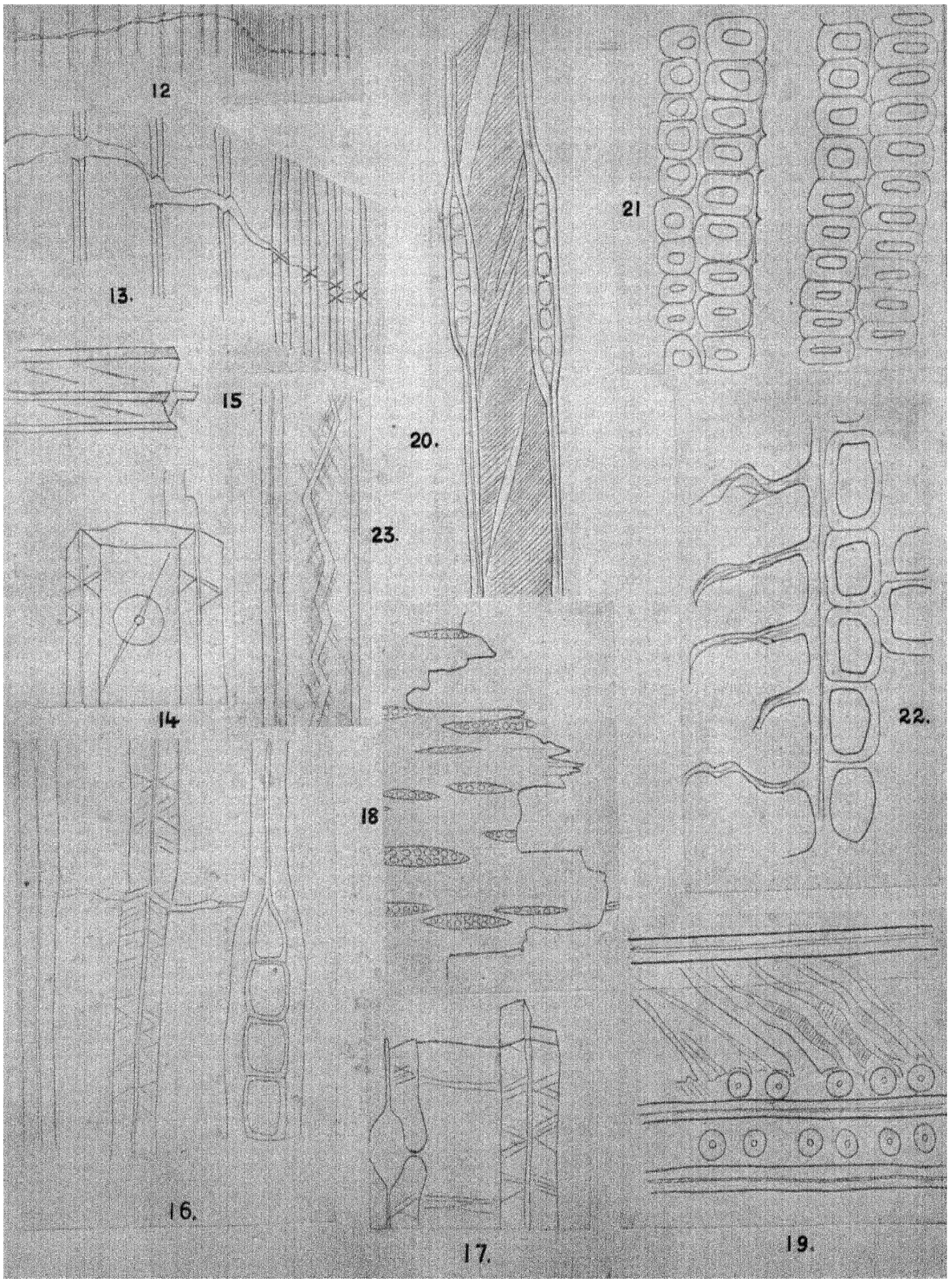

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Fig. 6.—Walls of tracheides of Spruce in radial section, showing oblique slipping lines both in the thickness of the tracheides and on the surface of the walls. The lines on the latter are not inclined at the same angle as the slits of the pits. × 275.

Fig. 7.—Walls of tracheides of spring wood of Spruce from same radial section as fig. 6, showing obliquity of slip-planes in the thickness of the walls and the horizontal character on the surface of the walls. × 275.

Fig. 8.—Walls of the tracheides of autumn wood of Pitch Pine in tangential longitudinal section, showing multiplicity of shearing planes leading to buckling. × 600.

Fig. 9.—Walls of fibres of Ash, showing multiplicity of shearing planes leading to buckling. × 900.

Fig. 10.—Walls of autumn tracheides of Spruce, fractured in tension, showing fibrous character of the break owing to shearing having occurred both in the radial and tangential walls. The inclination of the planes of fracture is approximately that of the slits of the pits. × 600.

Fig. 11.—Walls of tracheides of spring wood of Spruce in same specimen as fig. 10, showing similar oblique planes of fracture. An incipient fracture is also seen developing along similarly inclined planes at S. × 600.

## Plate 4 (Drawings).

Fig. 12.—Walls of tracheides of autumn and spring wood of a brittle piece of Spruce, showing tension fracture spreading across them. × 80.

Fig. 13.—A few of the walls shown in fig. 12. Rupture has occurred in the spring tracheides, and the development of a very few slip-lines is seen in the autumn tracheides. × 275.

Fig. 14.—Walls of tracheides of autumn wood of Spruce, showing the horizontal break on surface of wall and oblique break in the thickness of the wall along slip-planes. The inclination of the slits of the pits is indicated. × 600.

Fig. 15.—Fractured ends of fibres of Ash. The break is along the oblique slip-planes, which are not inclined at the same angle as the pits. × 275.

Fig. 16.—Tracheides of Pitch Pine, fractured in tension. The break has occurred along slip-lines which are developed also in the vicinity of the rupture. × 600.

Fig. 17.—Walls of tracheides in fractured tension specimen of Pitch Pine, showing slip-lines. A bordered pit is shown, and this clearly has not proved a source of weakness. × 600.

Fig. 18.—Tension fracture of Ash (somewhat diagrammatic). The break has had no obvious relation to the medullary rays. × 80.

Fig. 19.—Radial longitudinal section of a specimen of Spruce, fractured by shearing along a tangential plane. The shredding of the walls is seen and also the fine slip-lines on some of the shreds. The bordered pits are intact, and only a narrow zone of the wall is stretched out—*cf.* width with that of the adjoining tracheide. × 275. (*Cf.* with Plate 3, fig. 11.)

Fig. 20.—Walls of tracheide from fractured region of a specimen sheared in the radial plane. Stretching of the wall has occurred with incipient shredding and the development of fine lines of slipping. × 275.

Fig. 21.—Transverse section through autumn wood of fractured specimen sheared in radial plane. The separation has occurred at the middle lamella. × 275.

Fig. 22.—Transverse section through the spring wood of the same specimen as in fig. 21, showing the drawing out of the tangential walls into shreds. × 275.

Fig. 23.—Walls of tracheide from fractured region of specimen sheared in the tangential plane. Separation is taking place along two series of obliquely inclined planes. × 275.

# III.—*On a Form of* Botrytis cinerea, *with Colourless Sclerotia.*

*By* William B. Brierley (*Rothamsted*).

*Communicated by* Dr. E. J. Russell, *F.R.S.*

[Plate 5.]

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## 1. Introduction.

*Botrytis cinerea* is perhaps the commonest and best known fungus, and has been a centre of mycological research since the time of de Bary. Few, if any other fungi, have been studied so thoroughly by so many able investigators, or are the subject of so extensive a literature; and one need only draw attention to the researches of de Bary (6), Pirotta (61), Marshall Ward (80), Kissling (45), Nordhausen (58), R. E. Smith (70), Farneti (27), Beauverie and Guilliermond (9, 10), Istvanffi (33), Reidemeister (65), and the more recent researches from the laboratory of Prof. V. H. Blackman (13, 16, 17, 84). There is a body of experimentally ascertained and exact knowledge concerning the bionomics of this fungus, which can be exceeded by that of few other micro-organisms.

For the particular purposes in view in my investigations, it has been imperative

that all experimental work be carried out with pedigree cultures. It was very early discovered that the ordinary "pure-culture" of mycological and bacteriological laboratories may be and very often is a poly-genotypic population, and that very considerable genotypic differences may usually be found in apparently homogeneous populations exhibiting only one single type, around which the individuals fluctuate. In order to eliminate this vitiating factor, single-spore cultures were prepared either by BURRI's (19) Indian-ink method, plate isolation, or, more usually, by a combination of the plate and dilution-drop method. These cultures served as the initial source of experimental material. In all, over seventy such pedigree stocks have been prepared from original sub-strata, representing about sixty different species of host plant, derived from all parts of the country. From these stocks some fifteen thousand cultures have been made. During the course of the investigation, many of these have been subjected to the most diverse environmental conditions, and all have been maintained under the closest scrutiny. With the exception of the single culture to be described, no change that could be interpreted as a permanent heritable alteration or mutation has been observed.

## 2. LIFE CYCLE OF *Botrytis cinerea*.

In nature, the fungus usually appears as a delicate smoke-grey velvety pile, covering diseased plant tissues or organic *debris*, or, on more resistant sub-strata, in the form of isolated grey pustules. This superficial growth consists of the branched conidiophores bearing spores. On germination, which under favourable conditions occurs in a few hours, each of the latter gives rise to a mycelium, which in two or three days produces a further crop of conidiophores and spores. When old, the hyphæ and spores may produce microconidia, which germinate directly giving rise to mycelium. If at any stage of development conditions unfavourable to sporogeny intervene, the mycelium produces sclerotia, and these, under more favourable conditions, give rise to tufts of conidiophores bearing spores. Under certain adverse conditions, the hyphæ may produce chlamydospores, or themselves break up into oïdia, and these, on germination, give rise to normal mycelium.

It was the opinion of DE BARY (5, 6), VIALA (79), ZOPF (89), and other early investigators, an opinion based purely on superficial resemblances and the frequent contiguity of growth of the organisms, that *Botrytis cinerea* is only the conidial phase of a Discomycetous fungus, which was referred to either *Sclerotinia Fuckeliana* or *S. libertiana*. In the absence of any proof of this connection, and despite their own negative experience, this opinion was accepted by MARSHALL WARD (80), KISSLING (45), and others, and so became an integral part of mycological literature. In 1905, ISTVANFFI (32) published a voluminous memoir, purporting to bring forward proof of the genetic relationship of *Botrytis cinerea* and *Sclerotinia Fuckeliana*. In spite of the prior and much more incisive work of R. E. SMITH (70), this evidence has been generally accepted. It is, however, of

doubtful value, for a critical examination of the investigation makes clear that ISTVANFFI has confused two distinct fungi, which possess certain superficial resemblances, often grow together on the same host, and are not easily separable in culture.

Recently, SEAVER and HORNE (68) claim to have established the relationship of an unnamed species of *Botrytis* with a new species of *Sclerotinia*, which they have termed *S. Geranii*. The evidence is very brief, and awaits confirmation, and, in view of the fact that many "pure-cultures" of fungi are undoubtedly mixed populations, that *Botrytis cinerea* and various species of *Sclerotinia* and other genera harmonise perfectly in their growth when developing intermixed, both on natural hosts and on many artificial media, and that, unless specially searched for, the very minute microconidia of both forms are easily overlooked, and may act as a contaminating factor, one may perhaps hesitate to accept unreservedly this evidence. Furthermore, in my own study, some fifteen thousand cultures of various strains of *Botrytis cinerea* and nearly related "species" have been closely observed under the most varied environmental conditions, and much experimental work has been specially directed towards the elucidation of the genetic relationships of the fungus. I have, however, found no evidence indicating that *Botrytis cinerea* is in any way a developmental phase within the life-cycle of *Sclerotinia Fuckeliana* or genetically related to any other species of this genus. Repeatedly, strains of *Botrytis cinerea* and various species of *Sclerotinia* have been grown side by side by inoculating alternate quadrants of a plate culture, and, under all conditions, have remained separate. My experience merely confirms that of LIND (47), R. E. SMITH (70), PELTIER (59), PETHYBRIDGE (60), and others, who have paid special attention to this aspect of the problem.

*Botrytis cinerea* as a discrete entity is an asexual fungus, and the critical importance of a *Sclerotinial* relationship lies in the possibility which this introduces of a sexual process. If the organism be sexual, any single individual may possibly be heterozygous, and there is then no inherent improbability that segregation may occur, resulting in the appearance of apparently new forms which might mistakenly be interpreted as mutants.

In many *Mucorineæ*, *Chytridineæ*, *Saccharomyces* and possibly other *Ascomycetes* the sexual process is allogamous and factorial segregation is not impossible. In the great majority of fungi, however, in which sexuality occurs, and here is included so far as is known the entire group *Discomycetineæ*, which contains the genus *Sclerotinia*, the process is autogamous. Now it is well known, and has recently been mathematically demonstrated by JENNINGS (35), that even in an originally heterozygous organism, self-fertilisation if continued generation after generation leads rapidly to a condition in which the offspring are homozygous. In such case JOHANNSEN (36, 37) has shown that the mere isolation of the progeny from a single reproductive member produces a pure line.

Even, therefore, in the remote contingency that *Botrytis cinerea* is merely a developmental phase of *Sclerotinia Fuckeliana* and that this possesses a sexual process—which has yet to be demonstrated for any species of this genus—it would appear that the complications resulting from heterozygosis are absent from our problem. For critical purposes *Botrytis cinerea* is, on all evidential criteria, an asexual homozygotic organism in which the isolation of a single spore strain necessarily implies the isolation of a "pure-line." A genotypic change in a pure line is a mutation.

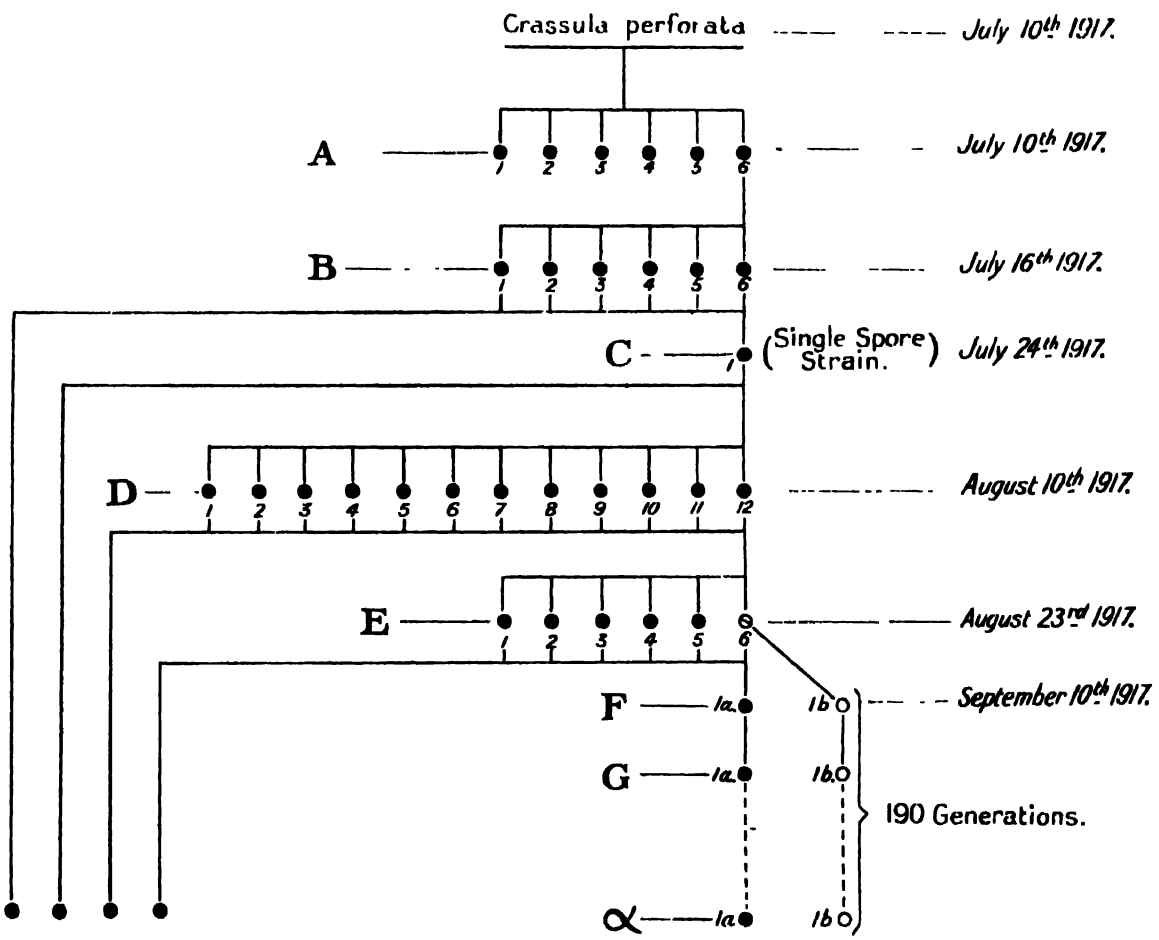
### 3. Origin of Colourless Form. General.

On July 10, 1917, a diseased specimen of *Crassula perforata* from the succulent house of the Royal Botanic Gardens, Kew, was examined, and the causal pathogen identified as *Botrytis cinerea*. The growth was normal in every respect, and from it six cultures, (A. 1–6), were prepared. These appeared to be free from contamination by other organisms, and on July 16, six further cultures, (B. 1–6), were taken from (A. 6). On July 22 all twelve were carefully examined and found to be free from contamination. A series of dilution drops were then prepared from (B. 6), many of these drops containing but a single spore. The latter were transferred to a thin plate of potato-agar and their development scrutinised carefully during two days. A colony whose origin from a single spore had been ascertained with certainty was then picked up on a platinum wire and planted in a tube slant. The spores are comparatively large, the most common size on the host plant being $7{\cdot}5\ \mu \times 9{\cdot}5\ \mu$; they are thus easily seen and isolated. On germination they become still more obvious, and the obtaining of a single-spore strain is thus a simple procedure. On August 10 twelve cultures (D. 1–12), were prepared from the pedigree stock (C. 1), and on August 23 six further cultures, (E. 1–6) were made from (D. 12). So far the work had merely been a part of the ordinary laboratory routine, the cultures which were all on tube slants of potato-agar being used for various experimental purposes.

About a week later cultures (E. 1–6) were examined and some three or four days later re-examined. The six cultures had all been placed together in a wire basket and left on the laboratory bench. It was noted that in tube (E. 6) one of the sclerotia had not turned black like the others but had remained colourless. In certain strains of *Botrytis cinerea* these bodies do not form the black pigment characteristic of the genus until they are mature, and although this particular sclerotium differed from its fellows in apparently following this mode of behaviour, it was merely regarded as a somewhat youthful individual, perhaps a little unusual, but not particularly noteworthy. On September 10, however, when tubes (E. 1–6) were again examined and the aberrant sclerotium in (E. 6), now quite mature, was found to be still lacking any sign of pigmentation, it was decided to isolate this sclerotium and breed from it. In tube (E. 6) there were in addition to the colourless sclerotium 24 normal black sclerotia and a black sclerotial crust around the bottom of the tube, where the medium had contracted away from the glass.

The colourless sclerotium was removed and thoroughly washed in sterile distilled water to remove adherent spores. It was then broken open and a fragment from the centre taken out, placed on a tube-slant of potato-agar (F.I. *b*) and incubated at 22° C. A vigorous growth ensued and a week later sclerotia began to be formed. In the tube there were ultimately formed 17 sclerotia and all were colourless.

TABLE I.




In a normal sclerotium the pigmentation is confined to the outer one to three layers of cells (text-fig. 1) and as it is from these that the conidiophores arise on germination, it was considered not impossible that these cells and their derivatives only might carry the power of colour formation. If, therefore, a fragment of the inner hyaline tissues of such a normal sclerotium were planted on a nutrient medium it seemed possible that colourless sclerotia similar to those obtained in tube (F.I. *b*) might develop. Accordingly, a black sclerotium from (E. 6) was treated thus—exactly as the aberrant sclerotium had been treated. The subsequent culture (F.I. *a*) contained uniformly black sclerotia.

There were now in existence two distinct strains (F.I. *a*) and (F.I. *b*) of the fungus

both derived from a single-spore stock (C. 1). Of these the parental form (F.I. *a*) possessed the highly characteristic black sclerotia; whilst the new strain (F.I. *b*) which had arisen from this apparently by a single direct saltation, possessed colourless sclerotia. The history of the two forms is shown in a diagrammatic manner in Table I. The distinguishing lettering (A. 1–6) and so forth, and the arrangement of descent in this Table have been adopted for the sake of clearness in the account. In practice (D. 1–12) were merely 12 similar cultures taken from (C. 1), and (E. 6) was taken from one of these cultures chosen at random. In the same way six cultures were made on July 16 and from one of these chosen at random (C. 1) was prepared.

It seemed possible that an albinistic tendency might be a "weakness" inherent in this particular race of *Botrytis cinerea*, and that if the preceding generations were further subcultured colourless sclerotia might again appear. Unfortunately the original diseased plant and the first six cultures made from it had been destroyed, but all subsequent cultures had been retained. As no particular care had been taken of these some had become contaminated. In all cases, however, it was possible to subculture purely from them and this was done extensively for many generations under the most diverse conditions of light, temperature, food supply and so forth, all the resulting cultures being most carefully examined for any indication of a lack of sclerotial pigmentation. All were perfectly normal.

The parental strain and its colourless derivative have each, up to the time of writing, passed through over two hundred direct tube generations with very many lateral subcultures, and although these have been placed under diverse environmental conditions each strain has remained absolutely constant.

Since this colourless strain arose, many thousands of cultures and fresh specimens of *Botrytis cinerea* have passed under my observation, but in no single instance have I found any similar absence of sclerotial pigmentation. Prof. H. H. Whetzel, of Cornell University, who for some years has been engaged upon a monograph of the genus Botrytis and has received and compared material from many parts of the world, informs me, after having examined a culture of the colourless strain, that he has "never seen anything quite like it." In the voluminous literature devoted to the fungus there is no record of a form with colourless sclerotia.

Having regard, therefore, to our knowledge of the fungus *Botrytis cinerea* and to the particular conditions under which the aberrant strain originated, it would appear difficult on present criteria to interpret it as other than a true mutation.

### 4. Comparison of Parental Strain and its Colourless Derivative.

The obvious difference between the original and the derived forms lies in the colour of the sclerotia. Mutations in the fungi *Aspergillus niger* and *Penicillium glaucum* have been described at length by Arichovskij (2), Waterman (83) and Schiemann (69). In these cases, however, although the obvious change was in spore

colouration, there were other less visible changes in several independent respects, certain morphological characters and physiological activities of the derived fungi being different from those of the original forms. In addition to these facts, the results of recent researches on the linkage of characters and the multiple allelomorph interpretation of quantitative inheritance made it appear probable that in the present case the colour change might be only one of many related changes less obviously visible.

Moreover, whether one regards the black sclerotial pigment as a mere excreted product or as an integral and actively functioning substance in the metabolic activities of the organism, the pigment itself is the result of a long and elaborate series of causally dependent processes, and a sudden and permanent loss of the power to excrete or form such matter can only be the visible expression of deep-seated physiological changes in the developing organism. But a living organism is an extremely complex and delicate equilibration of rhythmic metabolic processes in a colloid substratum, and it is difficult to conceive of any sudden derangement of these activities which has not reverberations in many directions.

It seemed, therefore, very desirable to make some comparison of the parental strain and its colourless derivative to ascertain the nature of any changes other than pigmentation which might be present. This comparison proceeded along several lines, the main directions of which are indicated briefly below.

### A. *Physiological Activities.*

If, as evidence would seem to show, the physiological reaction of a particular organism is constant only in an unvarying environment, it follows that identity of response to like stimuli implies identity of constitution, and, conversely, that a change in physiological constitution will be reflected in a changed reaction to unaltered conditions. Only if this is true may a comparison of the physiological activities of two organisms be instituted; and being true, it will afford the most delicate test of individual or genotypic identity, for the technique is quantitative and the nicest differences may be measured.

(a) *Germination of Spores.*—The effect of the character of the nutrient medium upon the germination of fungus spores is often very marked, and not infrequently this relation may be used to differentiate two or more genotypes otherwise difficult to distinguish. The percentage germination within certain periods of time when the spores were immersed in distilled water, 15 per cent. gelatine in water, and COONS' solution (21) were compared in the two experimental forms and in two strains used as a control. The spores were taken from three-day cultures on potato-agar incubated at 22° C., and the hanging drops in which the germinations were tested were maintained in the cool incubator at 18° C. The results are shown below, the numbers representing percentage germinations.

| Medium. | Parental Strain. | | | Colourless Strain. | | | Control Strain A. | | | Control Strain B. | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 6 hours. | 12 hours. | 24 hours. | 6 hours. | 12 hours. | 24 hours. | 6 hours. | 12 hours. | 24 hours. | 6 hours. | 12 hours. | 24 hours. |
| Distilled water | 10 | 27 | 55 | 12 | 25 | 53 | 33 | 51 | 68 | 25 | 55 | 93 |
| 15 per cent. gelatine | 43 | 67 | 93 | 41 | 66 | 90 | 47 | 78 | 90 | 47 | 72 | 90 |
| Coons' solution | 63 | 83 | 97 | 61 | 80 | 96 | 63 | 90 | 98 | 61 | 72 | 98 |

The lethal temperature of the spores was tested by making spore suspensions in 15 per cent. gelatine in distilled water and heating corresponding tubes of parental, derived, and control strains together in a water bath for ten minutes, the temperature rising by increments of five degrees. The experimental strains both gave growth in tubes heated to 45° C., but not in those heated to 50° C., whilst in the control tubes growth was inhibited by temperatures of 45° C. and 55° C. respectively.

(b) *Growth on Nutrient Media.*—One of the most critical and easily determined measures of the identity of two fungi is their growth and behaviour upon various standardised nutrient media under controlled conditions. The general characters of the colony, the colour reactions of hyphæ and medium, and the many other detailed phenomena which may be observed are valuable diagnostic characters, and sharply reflect the physiological differences separating two genotypes. At the end of his paper on "Cultural Studies of Species of *Penicillium*," THOM (77) has drawn up a scheme of comparative cultural data, which, in the present absence of any more detailed formulation, could with valuable results be adopted by mycologists as a basis of systematic diagnosis. In the comparative examination of the experimental strains this technique was followed, and the results compared with those of two control strains. No essential difference could be detected between the former, but these stood in marked contrast with the latter. For laboratory purposes other than this particular investigation, the parental strain and its colourless derivative were largely used in experiment, so that the cultural comparison of the two forms was amplified in very many ways. In all cases where they were grown under parallel conditions no essential difference could be detected. The comparative development of the two strains and control cultures was tested further at various temperatures, and with different intensities of light and conditions of aeration, but the results obtained only confirmed those referred to above.

A few qualitative experiments were carried out to test the comparative enzyme production of the fungi, the methods used being adapted from those described by CRABILL and REED (22) in 1915. On starch-agar the experimental strain and one control showed approximately equal amylolytic action under the colonies, while the second control showed a distinct halo indicating the presence of a diffusible extra-

cellular amylase. These differences were thrown up more clearly when the plates were flooded with iodine solution. On litmus-cream-agar growth of the experimental strains was profuse, and there was strong acid production, the red colour diffusing through the medium. In both control strains the lipolytic action was equally marked but the redness much more sharply defined. All the four strains liquefy gelatine and slowly dissolve fibrin in fibrin-agar. In both experimental strains the lipase production is feeble and only slight browning of the fibrin occurred, this being markedly different from the results in the controls. On casein-agar moderate growth occurred, and ereptic action was prominent, extending in a distinct band around the colonies. The production of erepsin was distinctly greater in both controls than in the experimental strains. Sparse development occurred on asparagin-rosolic-acid-agar with slight amidase production. The red colour in the experimental strains was less diffuse than in the controls.

Cytase formation was tested by growing the organisms in Dox's solution (23) the carbon source being filter paper. Moderate growth occurred, but after a fortnight there was only a barely perceptible reduction with FEHLING'S solution in the experimental strains and one control strain, whilst the second control showed more distinct cytolytic action. Calcium-carbonate-agar prepared with Dox's solution (23) plus one per cent. of lactose showed a feeble though distinct production of lactic acid, this being more marked in the experimental than in the control strains. In all the experiments no essential differences in the enzymic activities of the normal strain and its aberrant form could be detected.

(c) *Pathogenicity.*—Marked and constant differences in virulence for different hosts are shown by the various strains of *Botrytis cinerea*. In testing the comparative pathogenicity of the experimental strains, the spores, together with a fragment of potato-agar, were planted on corresponding surfaces such as the opposite sides of a fruit, or opposite halves of a leaf. On banana, apple, and tomato fruits, lily and potato leaves, tulip bulbs, and twigs of horse-chestnut infection readily occurred, and vigorous development ensued. On onion-bulb scales, potato tubers, crab-apple, cucumber, and fruits of *Pyrus japonica*, leaves of *Primula sinensis* and wall-flower, infection occurred with very considerable difficulty and only when the tissues were badly bruised, and the growth tended to die out rapidly. Bulbs of snowdrop and leaves of Portuguese laurel and rhododendron could not be infected. In no case was any essential difference in pathogenicity noted between the parental and colourless strains. Markedly different results were obtained with the two control strains, of which one was originally derived from onion bulbs and the other from fruits of *Pyrus japonica*.

The cultural examination of the parental strain and its colourless derivative, although put separately above, was only part of a much larger series of experiments which were being carried out in the laboratory to ascertain the physiological differences of closely similar morphological strains, and the identity of result obtained

in this comparison very largely takes its critical value from its relation to this wider issue. Briefly, it may be stated that so far as the physiological constitutions of the parental strain and the colourless strain may be judged from their behaviour, the two strains are identical.

### B. *Morphological Characters.*

Phenotypic plasticity is shown by most fungi, and is not only evident in those general characters which together constitute the morphological facies of the organism, but in those critical structures, the reproductive bodies, whose constancy has so often been assumed.

(d) *Dimensions of Spores.*—During recent years it has been shown in a general way by many students of the fungi, notably perhaps by Stevens and Hall (76), and following their investigations by Elliott (26), Moreau (53), Mutto and Pollacci (57), Gäumann (30, 31), and others, that the size of fungus spores is a function of the particular organism and the environmental conditions. With regard to the present fungus, *Botrytis cinerea*, under certain standardised conditions, the spore dimensions are a function of the particular pure line and the quality of the nutrient substratum; and for any particular pure line, different standardised food-media give different but mathematically constant quantities for the modal values of the variation curves of the spores. On a series of standardised media under constant conditions, therefore, the modal values of the spores of any pure line of the fungus may be represented by a curve which is constant and characteristic for that pure line. The critical quantity is not the extremes of variation, but the curve of modal values; and, other factors not varying, a difference of genotype is immediately reflected in this curve of modal values.

The modal values of the spores of the parental strain and its colourless derivative were compared in this way, the number of measurements for each particular test being 500. The results of three such comparisons are shown on p. 93.

The conidiophores of the fungus are comparatively large and complexly branched structures, and the mechanical difficulties in the way of their minute comparison are such as to render it difficult to eliminate errors of selection. In so far, however, as these structures could be compared with regard to the length, diameter, manner of branching and abstriction of spores no differences could be distinguished between the normal strain and its aberrant form; and this holds true also for the colour of the spore mass.

(e) *Haptera.*—One of the most interesting structural features of *Botrytis cinerea* are the organs of attachment, which were described by de Bary (5, 6) under the name "Haft-organen," and are variously termed "haptera" or "appressoria."

Their presence or absence in a culture is determined by environmental conditions, and the controlling factors are different for the several strains of the fungus. The experimental strains behaved similarly in this respect, forming few haptera when

| Medium. | Spore. | | Parent. | Derivative. |
|---|---|---|---|---|
| Potato-agar | Length | Minimum | 6·0 u | 6·0 u |
| | | Mode | 9·5 u | 9·5 u |
| | | Maximum | 12·0 u | 12·0 u |
| | Breadth | Minimum | 4·5 u | 5·0 u |
| | | Mode | 7·5 u | 7·5 u |
| | | Maximum | 10·0 u | 10·0 u |
| Steamed potato | Length | Minimum | 6·5 u | 6·5 u |
| | | Mode | 10·5 u | 10·5 u |
| | | Maximum | 16·0 u | 16·5 u |
| | Breadth | Minimum | 5·5 u | 5·5 u |
| | | Mode | 9·0 u | 9·0 u |
| | | Maximum | 13·5 u | 14·5 u |
| Czapek's medium | Length | Minimum | 6·0 u | 6·0 u |
| | | Mode | 11·5 u | 11·5 u |
| | | Maximum | 17·0 u | 17·0 u |
| | Breadth | Minimum | 5·5 u | 5·0 u |
| | | Mode | 9·5 u | 9·5 u |
| | | Maximum | 14·0 u | 14·5 u |

incubated at 22° C. on CZAPEK's medium lacking carbon, producing them in abundance when M/10 glucose is added to this medium, and suppressing their formation when M/1 glucose is added. A similar course of behaviour is evident when the substratum remains constant and the temperature varies. The particular relations between hapteral formation and controllable external factors are very individual for the several strains of *Botrytis cinerea*, and constitute a diagnostic feature. The identity of behaviour between the normal strain and the colourless strain is therefore noteworthy.

(f) *Sclerotia.*—The type of correlation between hapteral formation and environment which has been indicated above holds true in the formation of sclerotia, and the presence or absence of these in any particular strain may be determined at will. It may briefly be stated that under all circumstances the modes of behaviour of the two strains with respect to this structure were alike.

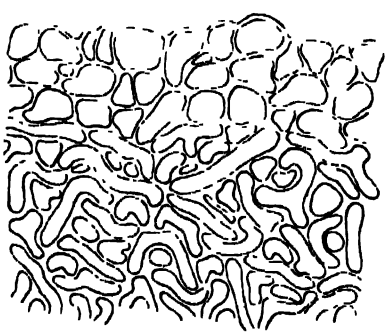
Owing to the widely held belief regarding the constitutional weakness of albinos, as compared with the normal type, it was considered not improbable that the colourless sclerotia might show a lack of vitality and power to withstand adverse conditions. No indication of such weakness had appeared in the general cultural comparison of the two strains, but it seemed desirable to test the sclerotia themselves, for it is a common assumption that dark coloured or "carbonised" hyphæ are more resistant than hyaline hyphæ. The comparison was made by testing the relative germinative capacity of selected black and colourless sclerotia after subjection to various treatments. Parallel series exposed to extremes of temperature and desiccation for various periods exhibited no differential resistance, nor was this found on subjecting

the sclerotia to saturated atmospheres of chloroform and ether, or various dilutions of toxic substances such as mercury bichloride, copper sulphate, carbolic acid, and picric acid. Other strains used as controls gave markedly different results.

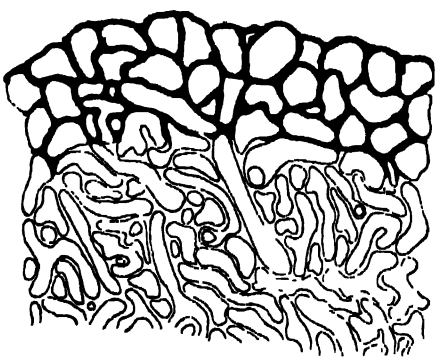
In structure the sclerotia vary according to the conditions under which they are formed. In contact with a hard surface they show an outer compact zone two or three cells in thickness which merges into an inner zone consisting of a firm colourless tissue-mass formed by closely interweaving hyphæ (text-fig. 1). On a soft matrix a third central zone of loose spongy hyphæ is usually present. The latter type of sclerotia are more or less spherical in shape whilst the former often fuse



1



2



3

TEXT-FIG. 1.

1. Vertical sections of colourless and normal sclerotia. Diagrammatic.
2. Vertical section of colourless sclerotium.
3. Vertical section of normal sclerotium.

} Swift $\frac{1}{8}$ obj. No. 4 eyepiece.

together into a thin concave crust. The contact surfaces of both forms are colourless, but this is merely due to lack of aeration, for if the sclerotia be removed so that all surfaces have access to air, the previously colourless contact surfaces develop the tissue containing the characteristic pigment. If, however, the sclerotia be cut across so that the inner tissue zones are exposed, these do not develop pigment. The power of colour formation is therefore confined to the peripheral cells. Save for the absence of pigment in these cells, the most minute examination of the structure and form of the sclerotia of the parental strain and its aberrant form failed to reveal any difference.

Like the physiological examination the comparison of the morphological characters of the two forms under discussion has greatly increased value when it is realised that this work was only part of a wider series of experimental researches, which functioned as controls, and the results of which were invaluable in aiding in the

interpretation of doubtful phenomena. The conclusion drawn from the entire study was that the parental strain and the aberrant derivative differed in respect only to the one character of sclerotial pigmentation. The phenomenon would thus appear to form an exact parallel with mutations by loss of single genes in the higher organisms, and it would stand in contrast with the fungal mutations described by ARCICHOVSKIJ (2), SCHIEMANN (69), and WATERMAN (83), in which there was simultaneous variation in several independent respects.

The explanation of an apparent genotypic alteration on the basis of such a profound change as the sheer "dropping out" of an element from a most delicately balanced reaction-system would appear out of the question. I can only visualise the organism as a unity in itself, in the sense that it consists of a very great number of elements, each an elaborate reaction-system, which bear a specific and causal relationship to one another. The continued harmonious functioning of the total system minus one of its parts is to me unthinkable.

Pure lines of organisms are often separated by characters which are extremely minute and difficult to detect, as for example the obscure serological reactions which differentiate certain races of bacteria, and it would appear probable that were the analysis in the present case carried to a further degree of refinement, many deeply underlying and elusive physiological differences between the two strains would be detected. Such work, however, would constitute a most laborious and intensive study quite beyond the scope of the present paper.

### 5. ORIGIN OF COLOURLESS FORM. SPECIAL.

A question of some considerable importance is the exact point of origin of the colourless strain. As described it apparently arose in the single colourless sclerotium found in tube (E. 6), and for long no doubt was entertained that this was its actual point of inception. In the absence of further evidence, however, there was no certainty of this, for the colourless strain would only be observed on the production by it of sclerotia, and if sclerotia were not formed the presence of this strain could not even be suspected.

Cultures (D. 1–12) had been made from the pedigree stock (C. 1) in the usual way, by transference of spores on a platinum wire, and a large and indefinite number of these reproductive bodies would thus be implanted in each tube.

Approximately 100 per cent. of these spores would germinate, and the resulting growth would therefore comprise very many intermingled mycelia, some or all of which would produce conidiophores and spores. Similarly, the six tubes (E. 1–6) of August 13, prepared in the same way from one (D. 6) of the previous twelve, would each contain an indefinite number of mycelia, each mycelium corresponding to a single individual. Each tube might, therefore, contain one hundred or more individuals of identical genotypic constitution, growing inextricably mixed together and all or few producing spores and later sclerotia.

Furthermore, the first crop of spores produced from the mycelia in the tube may fall to the surface of the medium, immediately germinate, and two or three days later again reproduce, when the same process may be repeated. Thus in each *test-tube* generation there may be two or more *lineal* generations, depending partly upon the conditions to which the growth is subjected, and partly upon the available germinating surface of the medium.

From the pedigree stock (C. 1) to the culture of August 13 (E. 6) containing the first colourless sclerotium there were present three direct test-tube generations, which may actually consist of from about six to twenty lineal generations, and at some one point in this series of life cycles the aberrant strain may have arisen. In the series of cultures under consideration there was no evidence that any accessory spore form was produced, nor were the conditions such as would be conducive to their formation. A brief discussion of the two possible points of origin, the spore and the sclerotium, is perhaps desirable.

### C. *Spore Formation.*

It will be clear that the colourless strain may have arisen as a variation in a single spore at any point between the second lineal generation in tube (C. 1) and the last lineal generation in tube (E. 6). If, for example, in the former, none of the offspring of this spore, although present in the later cultures, produced sclerotia until a favourable opportunity occurred in tube (E. 6). As, for essential purposes, the colourless form differs from the parental form only in the absence of sclerotial pigmentation, the presence of the former could not possibly be ascertained in a culture of the latter in the absence of the formation of its sclerotia. If, therefore, the aberrant form arose as a single spore variation, it is impossible to locate exactly its point of origin.

Certain facts relevant to the foregoing must, however, be noted. It has been an invariable technique throughout the whole of the research, when transferring inoculum from one tube to another, to take this either from a single conidiophore or, preferably, from a single germinated sclerotium. Now, every conidiophore and each sclerotium arises not only from a single original spore, but actually takes origin in a single mycelial cell. It will be obvious that this very considerably narrows the range wherein the aberrant form may have arisen as a spore saltation.

Furthermore, from its inception the colourless strain has been constantly reproduced by means of spores, and if it arose as a spore variation, the very existence of the new form implies that this particular spore germinated and produced a mycelium giving rise to conidiophores and spores, the latter possessing the new potentiality. But a single mycelium gives rise to an immense number of conidiophores, and the number of spores produced on even a single conidiophore is very great. It is, therefore, almost unthinkable that the new character should not again have appeared in any of the direct and lateral cultures made from tube (E. 6) and from the previous generations.

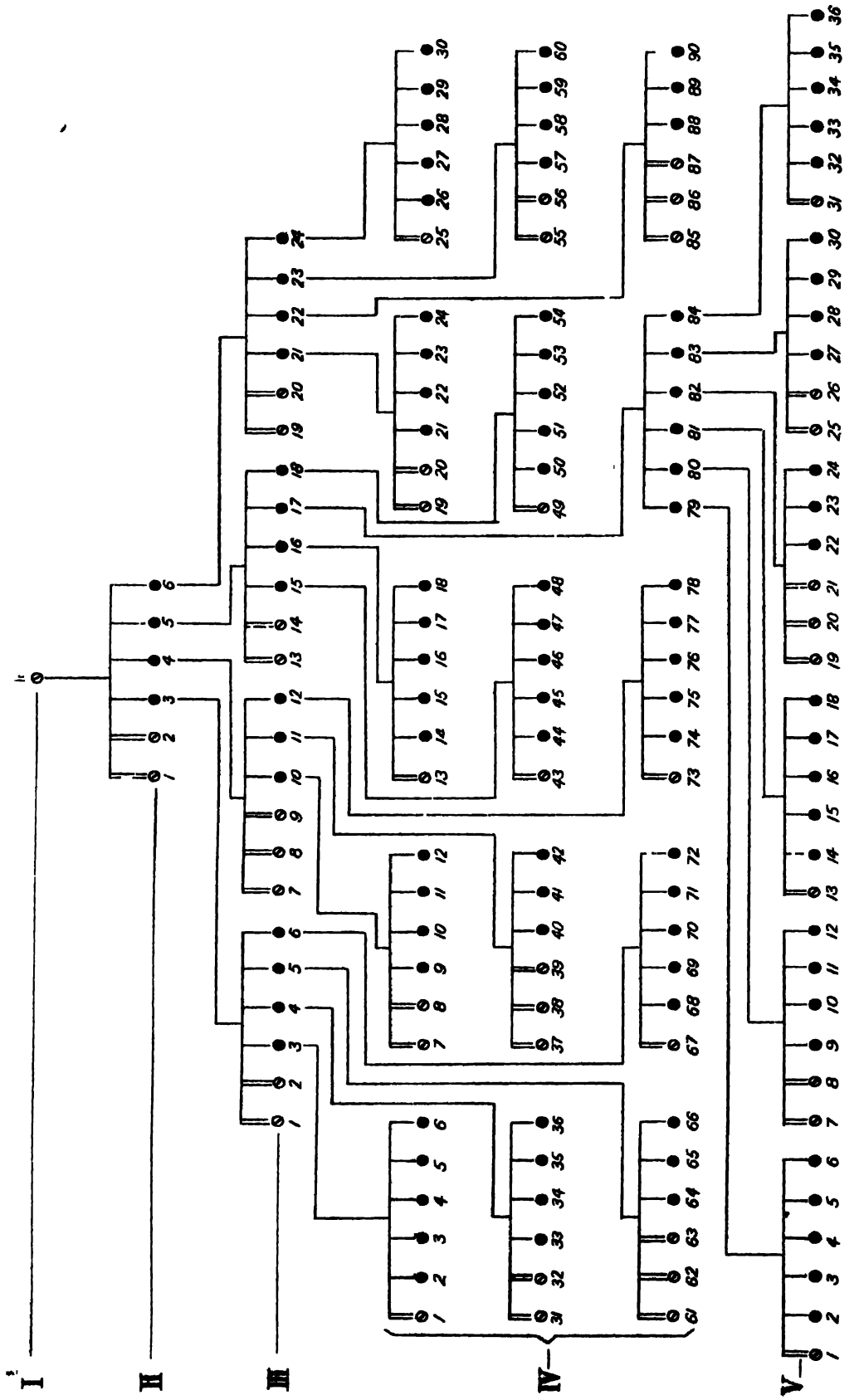
For purposes other than this particular piece of investigation it was decided to test the probability of the "throwing up" of the colourless strain in a parental culture, when only a single spore of the former is present. Accordingly, inoculum from (E. 4) was transferred to a clean tube-slant and streaked over the surface, after which there was inserted a single spore of the colourless strain. The circumstances would thus correspond in all essentials to those in tube (E. 6) if the aberrant form had arisen as a variation in a single spore. The results arranged diagrammatically are shown in Table II.

Tube (I) was prepared on March 2 and ten days later, when the sclerotia were mature, it was found that of the 23 sclerotia in the culture 2 were colourless, the aberrant strain thus "throwing up" in the first tube generation. On March 9 cultures (II. 1–6) were taken from (I) and ten days later it was found that 2 of these contained sclerotia of both strains, the remaining 4 containing only black sclerotia. In (II. 1) there were 15 black and 1 colourless sclerotium, and in (II. 2) 27 black and 1 colourless sclerotium. From each of the tubes containing only black sclerotia (II. 3–6) six cultures were made (III. 1–24). Of these 24 cultures 9 contained both parent and colourless form and the remainder black sclerotia only. In the former there were 162 black and 17 colourless sclerotia. From each of the 15 tubes containing only black sclerotia 6 cultures (IV. 1–90) were prepared. Of these, 24 tubes contained both black and colourless sclerotia in the proportion of 528 of the former to 39 of the latter, and the remaining 66 tubes contained only black sclerotia. In the 6 tubes (IV. 79–84), derived from (III. 17), only black sclerotia were present, and it appeared that in this line the colourless strain had "run out." To test if this were so, 6 cultures (V. 1–36) were made from each of these tubes. In at least 1 tube in each set of 6 the colourless strain was again thrown up, there being in all 10 tubes containing both kinds of sclerotia and 26 tubes containing only the black form. The work was not carried further than this; but in the total experiment, which represented 5 tube generations and 157 cultures, the aberrant form appeared in 46 tubes. A parallel control series prepared with similar inoculum from (E. 4) was synchronised with the foregoing, similar in all respects save that the single spore of the colourless strain was omitted. All the sclerotia were black.

It will be clear from this experiment that the presence of a single spore of the aberrant strain in a parental tube may cause the new character to appear in the first generation, and in a large proportion of cultures of succeeding generations. As already stated, the generations (C. 1), (D. 1–12), and (E. 1–6) were all subcultured freely, but the aberrant strain was absent from all descendants. In nearly 200 direct tube generations of the parent strain (F. 1*a*) the aberrant form has not appeared. This can only be explained by the hypothesis that the colourless strain did not arise as a spore variation, but arose in and was confined to the initial colourless sclerotium, and that the removal of this eliminated the aberrant strain from the parental culture (E. 6). The new strain was thus seen immediately on its inception and isolated.

TABLE II.

Inoculum from (E. 4) + one Spore from Colourless Strain.



### D. *Sclerotial Formation.*

It will be evident from text-fig. 1 that the sclerotium consists of a mass of more or less firm tissue, enclosed in a thin layer of cells, in the walls of which the black pigment is located. Now, unless the sclerotium arises in a single hyphal cell, in which the variation may have occurred, the physiological change resulting in loss of colour must have taken place simultaneously in all those peripheral cells which normally would form pigment. In view of the fact that the new character is strictly hereditary, and obtains by the growth of any portion of a single individual, and that the initial colourless sclerotium arose in a tube culture containing a perfectly normal growth, such a deep-seated physiological change occurring simultaneously in a very great number of cells, and to an identical degree in all, is a process extremely difficult to conceive.

Very little is known of the initial developmental stages in the formation of sclerotia, but the latter are usually considered to be a further growth or modification of haptera, structures which are very accurately delineated in the works of Marshall Ward (80) and Istvanffi (33). In their formation one, or more usually several related hyphæ form short branches on which arise tufts of secondary branches. These are directed vertically to the contact surface, and the clustered hyphæ mat together laterally forming a solid body of a tassel-like shape and structure.

It is of interest to note that de Bary (5, 6) regarded sclerotia and haptera as discrete bodies, stating that although clusters of haptera "have been mistaken for sclerotia . . . they have no connection." Munn (56), who has most recently investigated this fungus, writes: "It was observed that in many cases the appressoria are incipient stages of the sclerotia (Plate 3, figs. 23, 24)." Now if Munn's figs. 23, 24, and 13, which represent stages in the development of sclerotia, be compared with his figs. 25 and 27, which show the development of haptera, the essential difference is plain; and this distinction is obvious in the many delineations of these structures by previous investigators. There are no transition stages. The general laboratory study of the fungus and the relation of hapteral and sclerotial formation to various media and known conditions show that the structures are organs *sui generis*. This was confirmed in a very striking way by the development of these bodies in the aberrant strain. The haptera of the normal strain very rapidly become dark coloured and finally almost black, and this similarity of colouring with the sclerotia is in large part responsible for the confusion. In the case of the colourless strain, however, it is most helpful, for whilst the sclerotia have completely lost their pigment, the haptera have retained it, and thus in the one culture there co-exist the albinistic sclerotia and brown or olive-black haptera. This colour difference is distinctive from the inception of the two structures.

If therefore the sclerotia and haptera are discrete entities, the earliest stages that we know in the development of the former are the clusters of interweaving hyphæ

depicted by ISTVANFFI, MUNN, and others, and there is no reason why these should not have arisen in the branching of a single mother-cell. On searching selected cultures both by sectioning, and more successfully by mechanical teasing and *intra vitam* staining with neutral-red and methylene-blue, the initial stages were soon found. For the present issue, the main point of interest is that each sclerotium arises symphogenetically from an individual cell of the mycelium.*

On the open surface of a soft matrix the sclerotia usually remain separate, but if developed in a fissure or along a line of contact they often fuse to form a continuous crust. Figs. 50 and 51 on Plate 15 of ISTVANFFI'S memoir (33) are to be interpreted in this latter way. If mixed inocula of parental and colourless strains be grown, interesting composite sclerotial crusts may very rarely be obtained. In these there is no intimate mingling of hyphæ, but merely a lateral "grafting," and if such a composite sclerotium be germinated, the conidia and conidiophores, although indistinguishable, each reproduce purely their original parental type.

From the foregoing discussion it will be clear that the physiological change which resulted in the production of the aberrant form must have occurred in the mother-cell which gave rise to the initial colourless sclerotium in tube (E. 6).

## 6. NATURE OF LOSS OF COLOUR.

A detailed biochemical study of sclerotial pigmentation is beyond the scope of the present paper, but one may perhaps refer to certain simple experiments which throw some light upon the nature of the physiological change which has occasioned the production of the colourless form.

During the last two decades the pigmentation processes in animals and plants have been the subject of much investigation, and although this has followed the two distinct lines of biochemistry and genetics, the results have complemented each other in a quite remarkable way. The general trend of evidence would appear to lead to the view that the pigmentation processes throughout are essentially of an oxidatory nature with associated subsidiary or perhaps preliminary reduction processes.

Albinos have been shown to be divisible into two categories termed "dominant whites" and "recessive whites" respectively. In the latter, the absence of pigment is due to the lack of either the oxidase factor, or the chromogen factor, or of both; whilst in the former, both oxidase and chromogen are present, but their interaction is prevented by a third inhibiting factor. The oxidatory nature of the pigmentation processes is common to so many widely diverse organisms, that one might with some justification expect to find it even in the fungi, and consequently to find also that albinism in such an organism as *Botrytis cinerea* showed common features with the same phenomenon in rabbits or primulas. This fungus, however, is asexual, and the terms "dominant" and "recessive" are inapplicable; but if the pigmentation

* In certain strains of *Botrytis cinerea* the sclerotia originate meristogenetically.

processes are parallel to those of other organisms, the physiological changes which have resulted in the production of the colourless form may involve either the presence of a new inhibiting factor or the loss of either oxidase or chromogen or both.

The simplest and most direct method of examining the condition of the aberrant form is to test the colourless sclerotia for the presence of oxidase. If this be present and active it follows that the chromogen factor must be absent for otherwise pigmentation would have ensued. If there is no oxidase reaction, then either this factor is lacking or its activity inhibited by a third factor. The technique was based on that devised by KEEBLE and ARMSTRONG (41, 42, 43) in their investigations of flower pigments. Solutions of benzidine, $\alpha$-naphthol, and $p$-phenylenediamine gave a marked reaction, whilst with a solution of guaiacum-resin a barely perceptible lavender-blue colour was obtained.

These reactions were unaltered by preliminary treatment of the sclerotia with absolute alcohol or hydrocyanic acid, or by the subsequent addition of hydrogen-peroxide, and in all cases they were produced in a few minutes irrespective of temperature differences ranging from that of the laboratory to incubation at 37° C.

The distribution of the oxidase in the colourless sclerotia was identical in every case, and was noteworthy, being confined to the walls of the peripheral cells which in the parental form contain the normal black pigment. So exact was this agreement that some of the sections of colourless sclerotia treated with benzidine were barely distinguishable from sections of normal sclerotia.

Whether the colourless sclerotia have been formed in light or darkness makes no difference to the intensity of the oxidase reaction, nor is this changed by growth of the fungus at various temperatures or upon nutrient substrata presenting very different physiological conditions.

On WHELDALE'S view (85) the chromogens are flavones or flavonal glucosides. The presence of these bodies in tissues may readily be detected by the bright colour given on exposure to ammonia vapour, and the dull-green (or sometimes red-brown) colour with ferric-chloride. When these tests were applied to sections and pulps of the colourless sclerotia a totally negative result was obtained.

NEILSON JONES (39) has shown that even in certain recessive whites both chromogen and oxidase appear to be present, but that owing perhaps to their discrete distribution interaction is prevented. To test the possibility of this explanation of the albinism of the aberrant strain a number of sclerotia were boiled in 5 c.c. of 50 per cent. alcohol to destroy the oxidase, pulped, filtered and the filtrate evaporated to a few drops. Sections of the colourless sclerotia were then immersed in this and incubated at 27° C. No trace of oxidase reaction was observed, confirming the absence of chromogen in the sclerotia.

True brown and black pigments are of the very greatest rarity in the higher plants. MÖBIUS (52) however has shown that they do exist as in the spots on the alæ of Vicia Faba, but even here the colouring matter is dissolved in the cell-sap.

In thin sections of the normal sclerotia of *Botrytis cinerea* the pigment appears as a true brown-black. Furthermore, as shown in text-fig. 1, it is contained in the substance of the cell-walls and not in the cell-content which is perfectly hyaline. It thus differs very markedly from the usual plant pigments, and would appear to be more closely related to the melanotic pigments, certain of the melano-proteins existing dissolved in the keratin structures.

The mother substance of melanin is generally supposed to be tyrosin, this colourless chromogen being converted into a black pigment by the oxidising enzyme tyrosinase. If, therefore, the black pigment in the normal sclerotia be melanin, the aberrant sclerotia which presumably lack the factor for tyrosin should exhibit a tyrosinase reaction. The tests for oxidase already referred to are only for the detection of phenolase or laccase which BOURQUELOT and BERTRAND (14), ZELLNER (88), PRINGSHEIM (63), KASTLE (40) and others have shown to be almost universally present in fungi.

Tyrosinase is comparatively rare in its distribution in fungi. BERTRAND (11), however, has shown its presence in species of *Russula*, especially *Russula nigricans*, and LUTZ (49) in the stipes and pilei of *Gyromitra gigas* and *Disciotis parlata*; while more recently it has been demonstrated in *Lenzites sæpiaria* by ZELLER (87) and in various species of *Actinomyces* by DRECHSLER (24).

According to BOURQUELOT and BERTRAND (14) the best substrate for tyrosinase is tyrosin. Colourless sclerotia incubated at 18° C., 25° C., and 37° C. for 14 days in a saturated aqueous solution of silk-tyrosin gave a totally negative reaction, nor could this be changed by preliminary treatment with alcohol, ferrous sulphate or hydrocyanic acid or by subsequent treatment with hydrogen peroxide. A pulp of sclerotia, or sections, gave a similar result with this treatment.

CHODAT and STAUB (20) have advocated the use of *p*-cresol with the addition of glycin for the detection of the enzyme tyrosinase. Sclerotia immersed in this and incubated at 37° C. showed after many days a diffuse pale-yellow tint instead of the rich violet-blue reaction characteristic of tyrosinase.

In 1907 ABDERHALDEN and GUGGENHEIM (1) showed that N/100 hydrochloric acid permanently destroyed the activity of tyrosinase, but in the present case an immediate and direct oxidase reaction with benzidine was obtained after preliminary treatment of the colourless sclerotium with N/40 hydrochloric acid, although a strength of N/30 destroyed its activity.

It was found by BERTRAND (11) that tyrosinase could be differentiated from other oxidising enzymes by its lower lethal temperature, its activity being inhibited at 50° C. The oxidase in the colourless sclerotia is inhibited only by a temperature of from 80° C. to 85° C.

Furthermore BACH (3, 4) has shown that the pigment formed by the action of tyrosinase upon tyrosin may be oxidised further to a colourless compound by a dilute acid solution of potassium permanganate. The normal black sclerotia of *Botrytis*

*cinerea* remained unaltered when treated in this way. The black pigment is indeed extraordinarily stable, remaining apparently unchanged after boiling in concentrated acids and alkalies. When treated thus the stuff of the tissues disappears whilst the pigment remains as a most delicate gossamer-like cellular film. This stability immediately distinguishes the sclerotial pigment of *Botrytis* from other black fungal pigments such as the Aspergillin of *Aspergillus niger* which is soluble in hot water, or the colouring matter of *Daldinia*, *Hypoxylon* and various other carbonaceous Ascomycetes, which is soluble in alcohol.

The foregoing simple experiments only show (*a*) that the colourless sclerotia possess a direct oxidase system of the laccase type in a region corresponding exactly with that in which the black pigment is present in the sclerotia of the parental strain; and (*b*) that flavones or chromogens are lacking in the colourless sclerotia, or if present, they are inactivated in some way not understood. The experiments do not prove that the pigment in the sclerotia of the parental strain is due to the oxidation of a chromogen or that the aberrant strain has arisen by the loss or inactivation of a factor for chromogen. When, however, the above results are considered along with those of GORTNER (32), KEEBLE and ARMSTRONG (41, 42, 43) and others, which cumulatively form such positive circumstantial evidence, it is somewhat difficult to resist drawing the deduction that the albino strain of *Botrytis cinerea* has indeed arisen from the black parental form by the loss or modification of a factor for chromogen.

## 7. SIGNIFICANCE OF COLOURLESS FORM.

### A. *Discussion of Recorded Mutations.*

The essential facts in the preceding pages may be summarised as follows: The colourless form arose spontaneously without any evident relation to external conditions or stimuli, in a single sclerotium of a culture which on accepted criteria was a pure line. The new form is apparently differentiated from its parent in respect to a single character only, that of colour, and this albinism would appear to be associated with the absence of a factor for chromogen. The change has occurred once only, and has given rise to a form unknown in nature and perfectly constant under all conditions. It would seem possible to place only one interpretation on these facts, that of mutation, and accordingly when I was privileged to exhibit this form to the Linnean Society of London on April 3, 1919, I described it as "an albino mutant of *Botrytis cinerea*."

Previous records of mutation in the fungi fall into two groups. In the first are those changes in genetic constitution which appear to bear a direct and purposive relation to certain conditions which have operated during the development of the organism or that of the preceding generation. As an illustration may be instanced the permanent acquirement of the power to ferment lactose by an organism previously unable to form lactase, this change being brought about by the growth of

the organism or its progenitor upon a lactose medium. The second category of mutations includes those cases in which the genetic change is apparently quite fortuitous, and this group is divisible into two sub-groups. In the first of these the change is associated with certain conditions which interfere with the normal metabolic reactions of the organism. For example, by treating the organism with toxic substances, or by subjecting it to extremes of temperature or desiccation, various indeterminate morphological or physiological changes are induced, such as alterations in spore dimensions or coloration, or growth upon standardised media. In the second sub-group the changes occur spontaneously under, so far as may be judged, perfectly normal conditions of development, and this category would include the colourless form of *Botrytis cinerea*.

Of the purposive mutations the classical case perhaps is that described by Massee (51), in which *Tricothecium roseum* was changed into a virulent parasite by habituating it to a previously immune host. This research to which credence is still largely given was, even for the year 1905, so inexact in all critical details that it may be now be regarded as of merely historical interest. Results worthy of serious consideration are described in the researches of Salmon (66, 67) on the adaptive parasitism of *Erysiphe Graminis* by means of growth upon bridging hosts, or the parallel results obtained with various rust-fungi by Marshall Ward (81, 82), Freeman (28, 29), Johnson (38), Pole Evans (62), and others. In none of this work, however, were the experiments carried out with single-spore strains of the fungi, under the rigidly controlled conditions imperative in such work. Nor was it realised until the more recent researches of Mains (50), Brooks and Cooley (15), Lauritzen (46), and others, how vital are the effects of even minute changes in the light, temperature, age, or humidity relations of the host plants. The findings of Kidd and West (44) on the importance of physiological predetermination in the life of the plant may also have a very material bearing on questions of relative susceptibility or immunity of host plants to fungal attack, and indicate factors which will be extremely difficult to control. Apart, however, from such collateral evidence as this, the value of bridging species in changing the physiological characters of the fungus is not supported by the work of Biffen (12), and has been directly contravened by the researches of Reed (64), and of Stakman and his associates (71–74). After much intensive study of this subject, the latter conclude "... the writers have not been able to detect any mutation nor to induce perceptible evolutionary changes experimentally." With rare exceptions such conclusions are supported by the invariable experience of all the critical and accurate workers in more recent experimental mycology, and there would appear to be little doubt that when a pure line organism is examined by a careful investigator under rigidly controlled conditions, heritable alterations bearing a purposive relation to educative treatment are absent.

The recorded instances of non-purposive genetic changes in organisms induced by

exposure to unusual conditions are very few in number. In 1908 ARCICHOVSKIJ (2) described a form of *Aspergillus niger* with yellow-brown spores which arose in a culture of the black form growing in Raulin's fluid to which 0·0001 per cent. of zinc sulphate had been added. Four years later SCHIEMANN (69) obtained various mutants of *Aspergillus niger* by treatment of cultures with potassium bichromate, exposure to high temperatures, and so forth.

In the same year WATERMAN (83) caused *Aspergillus niger* to mutate by treatment with 2 per cent. galactose, rhamnose, or glucose, 1 per cent. boric acid, *p*-oxybenzoic acid, or dichloracrylic acid. A fungus which the author speaks of as *Penicillium glaucum* was also caused to throw mutants by treatment with any of the following substances:—*p*-oxybenzoic acid, salicylic acid, trichloracrylic acid, tetrachlor-propionamid, pentachlor-propionamid, and pyrocatechetic acid (pyrocatechuic?).

In all the above cases the new forms described differed from the parental fungi in many morphological and physiological characters, the most obvious being that of the colour of the spores. Furthermore, the production of the mutant forms was not a constant and specific reaction to certain definite chemical stimuli, but was merely a fortuitous circumstance resulting from the generally unfavourable conditions to which the organisms had been subjected. These were of such diverse nature that one might expect that almost any substance deleterious to growth or interfering with the metabolic processes in any way would produce similar results. Also not every culture subjected to these conditions gave uniform results over the entire growth, but only occasional cultures, and in these cultures only sporadic individuals, conidiophores or spores. Moreover, as SCHIEMANN (69) points out, mutations were also produced when the fungi were developing under favourable conditions.

Such results as these would have a somewhat indifferent reception if obtained in a physical or chemical laboratory. Their anomalous nature is stated clearly in SCHIEMANN'S paper as follows: "Die konstanten Farbmutationen sind beide auf mit $K_2Cr_2O_7$ versetzten Nährböden aufgetreten. Von einer spezifischen Wirkung des $K_2Cr_2O_7$ zu sprechen, ist trotzdem nicht möglich. Schon der Umstand, dass der Farbumschlag unter über 100 Kulturen mit $K_2Cr_2O_7$ nur zweimal stattfand, hier wiederum nicht die ganze Decke betraf, sondern unter vielen hunderten von Köpfchen nur einzelne, spricht dagegen. Ferner hat die *Proteus*-Mutante dieselbe Richtung eingeschlagen; diese aber ist aus Hitzekulturen, einmal mit, einmal ohne Zusatz von $K_2Cr_2O_7$ hervorgegangen. Endlich sind nach braun abändernde Kulturen des *Aspergillus niger* auch sonst gelegentlich beobachtet worden—wenn auch selten—ohne dass das Chromal zur Verwendung kam."

In a discussion of the causes of genetic variation, BATESON (7) has written: "The state of knowledge of this whole subject is . . . most unsatisfactory, chiefly for the reason that in none of the cases which are alleged to show a positive result have two observers been over the same ground, or as yet confirmed each other . . . I do not know a single case which has been established and confirmed in such a way that we

could with confidence expect to witness the alleged phenomena if we were to repeat the experiment."

In the work of ARCICHOVSKIJ (2), SCHIEMANN (69), and WATERMAN (83), mutant forms were produced so easily and with such a diversity of stimuli and simplicity of technique, that it seemed probable that a repetition of their experiments might produce the necessary confirmatory evidence. Accordingly single-spore cultures of two strains of *Aspergillus niger* and of two strains of *Penicillium Italicum* were prepared. (WATERMAN used "*Penicillium glaucum*," but as THOM (77) points out, this " name as used at present seems to be applied collectively to the common green forms, which under examination are quickly found to be not one but several species.") With these fungi, the experiments of SCHIEMANN (69) and ARCICHOVSKIJ (2), and certain of those of WATERMAN (83) (galactose, glucose, rhamnose, boric acid, and salicylic acid) were carefully repeated. Although modifications in the colour of the spores, general morphological facies, and physiological reactions were observed, these affected the whole growth operated upon and to an equal degree; but the reproductive bodies of the modified fungi, when returned to the original conditions, gave in every case the original result. These changes were phenotypic and not genotypic, and throughout the whole series of experiments not a single mutation occurred.

More recently, experiments have been carried out with another strain of *Aspergillus niger* isolated from the air, and with a strain of *Penicillium* (*roseum*?) from the soil, both these having been in culture in the laboratory for several months and repeatedly subcultured, although not derived from single spores. The fungi were subjected to rather gross treatment with various dilutions of toxic substances, such as silver nitrate, copper sulphate, mercury bichloride, lead nitrate, potassium acid phosphate, sodium chloride, and so forth, and then platings were made from these tubes. The resulting growths were perfectly normal.

In all work on the induction of genotypic alterations in micro-organisms, it is extremely difficult, even when the most scrupulous attention is given to every detail, to be quite certain that one has under control each of the almost infinite number of factors which may influence the results. Mycologists are only now beginning to learn how extremely complex and difficult to isolate such factors may be, and the researches of, for example, DUGGAR (25) and his collaborators on the physiology of certain fungi grown in culture media, or those of COONS (21) on the factors involved in the growth and pycnidium production of *Plenodomus fuscomaculans*, indicate the complexities underlying apparently the most simple physiological phenomena. Not the least interesting of the many experimental studies throwing light on the bionomics of *Aspergillus niger* are those of JAVILLIER (34) and of STEINBERG (75), in which it is shown how even such an unsuspected factor as the different quantities of zinc present in the glass of flasks, test-tubes, and other apparatus may vitiate comparative cultural studies of this fungus.

If, in the work of ARCICHOVSKIJ (2), SCHIEMANN (69), and WATERMAN (83),

accidental contamination, did not occur, one is almost forced to conclude that some accessory factor of an unrecognised nature must have been operative in their experiments; a factor absent in my own repetition of their work and absent from the studies of every other mycologist who has carried out critical experimental investigations on these fungi.

Furthermore, as has been pointed out, these investigators emphasise the fact that their mutations are not of the nature of specific reactions to definite chemical or physical stimuli, but only the results of a generalised interference with the normal course of life of the organism. Thus SCHIEMANN (69) says: " . . . so zeigt sich als ein Gemeinsames, dass in allen Fällen, wo derartige Farbänderungen auftraten, Störungen der normalen Lebens-verhältnisse vorlagen. Es ist deshalb der Schluss berechtigt, dass die Mutation in den beobachteten Fällen durch einen starken Reiz ausgelöst wurde." But the experience of other investigators demonstrates the extreme genetic constancy of species of these fungi even when placed for many generations under the most unfavourable conditions. Numerous workers have shown that the morphological facies and physiological activities of fungi may within certain limits be changed at will in the single generation, but in no case, with the above exceptions, have these phenotypic modifications had any effect whatever on the genotypic constitution of the organisms.

### B. *Alternative Interpretations.*

If the recorded cases of mutation in the fungi need not be accepted—and for my own part I do not feel compelled to accept them—how then is one to regard the colourless strain of *Botrytis cinerea*, which has been described in the present paper? Its fortuitous origin as a single sclerotium in a perfectly normal single-spore strain, whose development since its commencement is known, has already been emphasised. Under no conditions whatever, so far as is known, may the black sclerotial pigment of the parent strain, or the albinism of its derivative, be modified, and although other characters may show plasticity, no instance of a permanent alteration has been observed. Does the phenotypic constancy of the parental strain under constant conditions necessarily imply genotypic purity?

In the preceding account the parental strain has been spoken of as a " pure line," and on all accepted criteria this description is merited, for not only is it a single spore strain of an asexual organism, but it has been reproduced for most of its generations either by spores from single conidiophores or from single germinated sclerotia, both of which take origin in a single cell. In his work on 'Evolution by means of Hybridisation,' LOTSY (48) rightly insists that: " *Certainty of purity is a* conditio sine qua non *to obtain proof of the existence of mutation in living beings, just as chemical purity is a* conditio sine qua non *to obtain proof of the existence of mutability of the elements.*" Is there certainty of purity in the parental strain of *Botrytis cinerea* which gave rise to the colourless form? Further, is the fulfilment of such a

criterion possible in the fungi (or bacteria), and particularly in those forms for which mutation is claimed?

The only positive contribution to this subject is the work of BURGEFF (18), published in 1914, in which the results of the crossing of various forms of *Phycomyces nitens* are described. This fungus possesses a cœnocytic mycelium, containing numerous scattered nuclei. In the asexual form of reproduction spores are delimited within sporangial heads into which there have passed an indefinite number of nuclei. The multinucleate spores germinate and reproduce the cœnocytic mycelium. If, therefore, the original hyphæ are genetically impure, this condition will be maintained in all succeeding generations, for the sporangiospores merely reproduce the genetic condition of the hyphæ which give rise to the sporangia. Opportunity for genetic contamination occurs at sexual reproduction, for this process is merely a fusion of two multinucleate gametes to form a multinucleate zygospore, which on germination gives rise to a cœnocytic mycelium containing nuclei of both parental strains. There will be an equal chance for both types of nuclei to pass into the sporangia and be included in the multinucleate spores. A single-spore strain may thus be heterocaryotic. If now this form at sexual maturity fuses with a third form, and so on, the genotype of any particular isolation may be extremely complex. As, moreover, the sporangiospores are delimited and the walls of the zygogametes laid down without any apparent regard either to the condition, the number, or the position of the nuclei they separate, there is no absolute surety that two single-spore strains derived from an original single-spore strain will have the same genotype.

In such *Mucorineæ* it is, therefore, totally impossible to comply with the criterion of specific purity which is imperative in this issue. There is an almost equal lack of certainty of specific purity in the genera *Aspergillus* and *Penicillium*. The mycelium of these fungi is multicellular and each cell contains many nuclei. On asexual reproduction a vegetative cell gives rise to a conidiophore, and from this conidia are abstricted. The hyphal mother cell is multinucleate and these nuclei, by division and wandering, finally pass into the reproductive cells, these, in many species of the fungi, containing an indefinite number of nuclei. In other species the conidia generally contain but a single nucleus, but almost any preparation of such conidia shows multinucleate individuals.

A single-spore strain thus reproduces the genotype of its parent, and if the latter contains nuclei of different constitutions, this heterocaryotic condition will be maintained in the progeny.

Now, in the case of *Phycomyces*, genetic contamination occurs in the sexual process, for many of these forms are allogamous. There are, however, no species of *Aspergillus* or *Penicillium* known in which sexuality is necessarily allogamous, although there is no certainty that this type of reproduction may not occur, at all events, at intervals. We still know too little of what takes place in the sexual processes of either of these genera to make their discussion profitable; but given a

union of two parental mycelia only once in many thousands of generations, the mycelia of the offspring can afford no certainty of specific purity.

Moreover in any culture of a single-spore strain of either fungus it is not usually difficult to find two hyphæ which have come into contact, and the walls separating them have been auto-digested, giving cytoplasmic continuity. In a mixed growth of a number of strains these somatic fusions are also to be found, and although one is not able to state that fusions occur between hyphal cells of different strains, neither may the rare possibility of this be denied. If now from such a contaminated cell in *Aspergillus* or *Penicillium* a conidiophore were to arise, or either or both the sexual organs, the offspring of the reproductive bodies would be genetically impure, and asexual reproduction would only maintain this heterocaryotic or heterozygotic condition.

Thus even accepting the evidence of ARCICHOVSKIJ (2), SCHIEMANN (69), and WATERMAN (83), it by no means follows that the permanent changes they observed are necessarily mutations, for they may be interpreted in terms of genetic contamination, and in no case may these organisms comply with that criterion of "certainty of specific purity which is a *conditio sine qua non* to obtain proof of the existence of mutation." Although in this account very little reference has been made to bacterial mutation, there can be little doubt that the possibility of the rare occurrence of "somatic" fusions in these organisms places them out of consideration as subject organisms for the experimental induction of mutations.

Thus, according to the principle of parsimony, all so-called mutations in these groups of organisms may perhaps more wisely be interpreted in terms of the splitting of an originally impure genetic constitution or of gametic or somatic segregation from heterozygotes.

These considerations applied to the fungus *Botrytis cinerea* throw an entirely new light upon the value to be attached to the colourless strain. *Botrytis cinerea* possesses a multicellular mycelium, each cell of which contains many nuclei. The conidiophores are multinucleate and a small but indefinite number of nuclei pass into each conidium. Throughout the whole of the vegetative and reproductive mycelium the septa are laid down by a diaphragm-like growth from the hyphal walls, irrespective of the number or condition of the nuclei thus separated. Each conidium, therefore, merely reproduces the genetic constitution of the original cell of the mycelium in which its conidiophore arose. Many thousands of such asexual generations would, therefore, not alter the genetic constitution of the organism, and there is no sexual process. The possibility of genetic contamination is brought about by the occurrence of hyphal anastomoses. In the extremely rare chance of a fertile conidiophore arising from a cell contaminated by the nuclei or cytoplasm of a genotypically different individual lies, I believe, the explanation of the colourless form of *Botrytis* described. While this possibility exists, it is more consonant with the principles of scientific methodology to accept this interpretation than to formulate a mutational hypothesis of the origin of the aberrant strain.

Before concluding, a few words may perhaps be said concerning the *rôle* of the nucleus in the heredity of multinucleate fungi. The conidia of *Aspergillus*, *Penicillium* or *Botrytis* contain a variable number of nuclei, and yet if conidia are plated out the colonies which develop are essentially similar in physiological reactions and morphological properties for each particular species. It follows, therefore, that the exact number of nuclei which chance to be enclosed in each reproductive body has no bearing on the absence or presence of particular characters in the progeny, but is a purely fortuitous occurrence. What is vital, is, as BURGEFF (18) has shown, not the number of nuclei in each cell but the kind of nuclei present. Although the evidence on this point is meagre there would yet seem no reason to doubt that the structure of the nucleus in fungi is in general fundamentally similar to that in other organisms.

Following MORGAN (55) the chromosomes might thus be visualised as linear series of loci, like threaded beads. At each locus exist specific factors, making up a reaction system the elements of which bear a more or less specific relationship to one another. Thus, eight loci, representing the factor for black sclerotial pigment in the chromosomes of as many identical nuclei, would therefore have neither greater nor less visible expression than one locus in the chromosome of a single nucleus, or than 15 loci in the chromosomes of 15 nuclei in a single reproductive body. Increased number of nuclei does not signify a cumulative value for any particular character. But if owing to somatic fusion a hyphal cell containing eight nuclei with loci for black pigment became possessed of one or more contaminating nuclei from a genotypically different individual, and if this particular cell gave rise to a sclerotium, the characters of this sclerotium would be determined by the reacting systems of loci present in the two kinds of nuclei, the visible characters being the expression of the resultant of their interaction. The contaminating nuclei might find themselves in a cytoplasmic environment so foreign to their normal metabolism as to remain inert, or the locus for colour might be counterbalanced or cancelled by the locus for black in any one of the eight original nuclei, in which case the seven remaining nuclei would reproduce the original colour. In both cases the sclerotial characters would be wholly normal. On the other hand the loci in the invading nuclei might function as lethal factors, such as MORGAN (54) has shown to exist in the case of *Drosophila*, and development might be partially or entirely inhibited.

Again, the factors in the one system might react in many ways with those of the other system changing the physiological and morphological characters of the adult form so that apparently spontaneous variation in several independent directions might result, producing "mutants" such as those described by ARCICHOVSKIJ, SCHIEMANN and WATERMAN. The majority of the factors of the contaminating nuclei might remain inert, but one or more might react with certain factors in the original nuclei resulting in the inhibition of one or more of the latter. If, for example, the factor for chromogen were thus inhibited or destroyed the adult would be an albino similar to the new form of *Botrytis cinerea* described. If there are several factors for

colour, as would appear probable in the present instance, that associated with sclerotial pigmentation only might be inhibited, leaving unaltered the factors governing the pigmentation of spores or haptera.

On the other hand, it is not improbable that the contamination may be purely cytoplasmic, and the progeny of such a cell will therefore still be homocaryotic. The foreign cytoplasm, however, would create a new environment through which the nuclei would function, and this might so influence the development of the organisms as to alter materially the outward expression of one or more characters in the adult form. As the added cytoplasm would now be an integral portion of the organism, this changed expression would be permanent and heritable. It is thus possible for apparent "mutations" to occur in the fungi without any change in nuclear character. So far as the nucleus is concerned, regarding this structure as an entity distinct from the cytoplasm, the change would merely be phenotypic; but for the complete organism the change would be genotypic. It is perhaps in such purely cytoplasmic contaminations that apparent mutations in those organisms having uninucleate cells may be sought.

In the case under discussion, nuclear and cytoplasmic contamination must have occurred prior to the isolation of the single-spore strain, and yet the colourless strain arose only in the third tube-generation subsequent to this. If, however, one assumes a contaminated original strain, it is not inconceivable that in the fortuitous septation of the hyphæ, certain nuclei and cytoplasmic matter were separated, such that in all things save chromogen formation the resultant resembled the parental strain. The expression of this resultant would be an albino strain such as that described. Such a concomitance of conditions might well appear almost inconceivable, but the appearance of an albinistic strain of the fungus is equally almost inconceivable, for in the history of the genus as we know it it has occurred but once.

It would seem to me probable that the same concept which BATESON (8) and LOTSY (48) have formulated for the higher organisms may hold true for both fungi and bacteria, but here the recombination of genes may not only take place by sexual fusions, but also by direct "contamination" of one species by the nuclei and cytoplasm of another in vegetative anastomoses. New reacting systems of chromosomal loci impinge upon each other, and the resultant is the new form. This at first may be heterocaryotic, but if true sexual processes occur later, the offspring become homocaryotic but heterozygous. Such a hypothesis fits the facts and explains them as I think no other present hypothesis does.

It is not the possibility of mutation in the fungi (and bacteria) that is here denied, but rather the compulsion to accept that interpretation of the evidence as it now stands. As the facts present themselves to me, avenues of interpretation other than that of mutation are still widely open.

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## DESCRIPTION OF PLATE.

Fig. 1.—Petri dish culture in which the normal form and its colourless derivative have been grown. Pigmented haptera of the albino strain may be seen at the periphery of the culture in contact with the glass. × ⅔.

Fig. 2.—Vertical section of colourless sclerotium. × 250.

Fig. 3.—Vertical section of parental sclerotium. × 250.

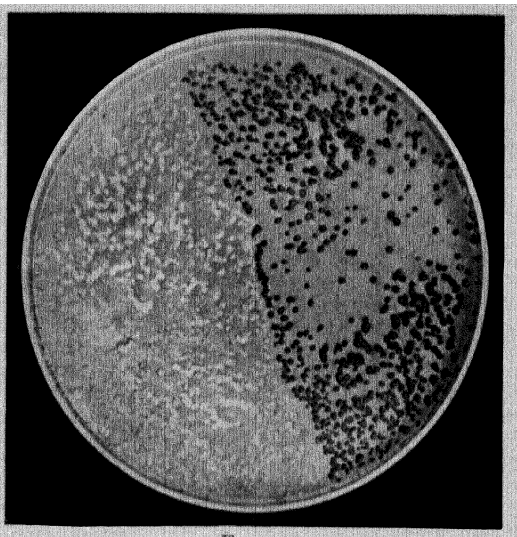


FIG. 1.

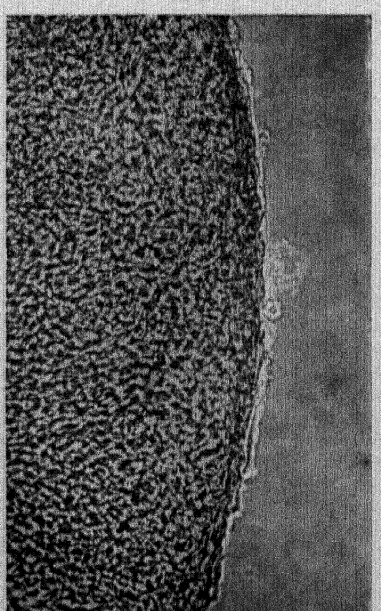


FIG. 2.

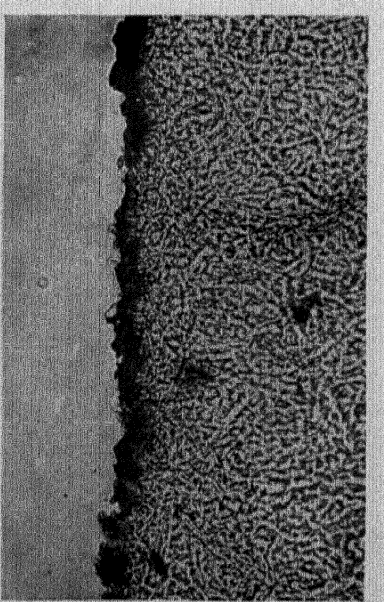


FIG. 3.

# IV.—*The Irish Eskers.*

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## I. The Theories of Eskers.

The term esker is Irish and its definition should be settled by reference to the eskers of Ireland. They are hills of sand and gravel, which are typically ridges, but are sometimes mounds or groups of mounds. Excluding various suggestions only of historic interest, there are three chief theories of the formation of ridge-eskers. According to the first theory, due mainly to Hummel (1874, p. 3), eskers are accumulations of gravel along sub-glacial rivers. According to the second theory, due largely to Holst (1876–7, p. 97), eskers are deposited along rivers flowing either over, or perhaps partially within, glaciers. According to the third theory, which was advocated almost simultaneously by Hershey (1897, p. 241), Baron de Geer (1897, pp. 377–386), and Baron von Toll (1899, p. 22), eskers are the deltaic deposits of glacial rivers, and their ridged form is due to their continuous deposition at successive positions by the slow recession of the river mouth during the retreat

of the ice sheet.* An esker so formed should show an annual banding due to the seasonal variations in the volume of the glacial river.† This banded structure is well developed in the Swedish osar (åsar), for many of which this receding delta theory may be regarded as established.

Prof. SOLLAS adopted HUMMEL'S theory for the Irish eskers. He described them (1896, p. 803) as the casts of systems of sub-glacial rivers. He justly objected to the supraglacial theory, since the eskers were clearly accumulated in their present positions (*ibid.*, p. 819) and had not been redeposited at a lower level on the melting of the ice. His map of the esker system of Central Ireland, compiled from the maps of the Geological Survey, shows some eskers arranged in convergent series like a river and its tributaries; and it was this arrangement which suggested the fluviatile origin of the osar of Sweden.‡ The Irish eskers have therefore been regarded as exactly equivalent to the Swedish osar.

The literature on the Irish eskers deals mainly with their distribution and general structure. It is therefore advisable, before considering their origin, to record some detailed evidence regarding their composition and intimate structure.§

## II. IRISH ESKERS.

### 1. *The Eskers near Tullamore and Kilbeggan.*

One of the most important and instructive esker systems is that of Ballyduff and Newtownlow, to the north and north-east of Tullamore. It has been described by J. O'KELLY and illustrated by DU NOYER, in 'Mem. Geol. Surv., Ireland,' Explanation Sheets 98, 99, 108, 109, 1865, pp. 29–32. JUKES, in the introduction to that memoir (p. 8), refers to this group as including "the most remarkable eskers yet mapped in Ireland." The esker has the plan of a horseshoe, situated around the town of Clara. Its north-western arm appears to be an extension of the well known Streamstown Esker, and its southern arm to be a continuation of the long east-and-west trending esker through Seven Churches and Ballinasloe. The plan of this esker system, as shown on Prof. SOLLAS's map (1896, Plate 69), appeared consistent with its formation by rivers which converged from the north-west, west, and south-west, and which continued eastward toward the Liffey through the two east and west

* VON TOLL clearly summarises his conclusions as follows:—"Die Bildung der Åsar am ehesten als das Product von Gletscherbächen anzusehen sind, die aus dem Thore eines Schritt für Schritt sich zurückziehenden Inlandeises hervorbrechen, oder mit anderen Worten als die Vereinigung einer Reihe auf einander folgender Schuttkegel" (1898, p. 22).

† I. C. RUSSELL (1893, p. 241) also adopted the view that the banding of eskers, or osar as he called them, was due to periodic variations in the streams.

‡ This arrangement is shown, *e.g.*, on the map by HUMMEL, 1874, Plate II, or in the figure by J. GEIKIE, 1894, p. 481.

§ The most detailed description is that in 'Mem. Geol. Surv.,' Sheet 112, of the Greenhills Esker, near Dublin, which is, however, especially in the part most fully described, not a typical example.

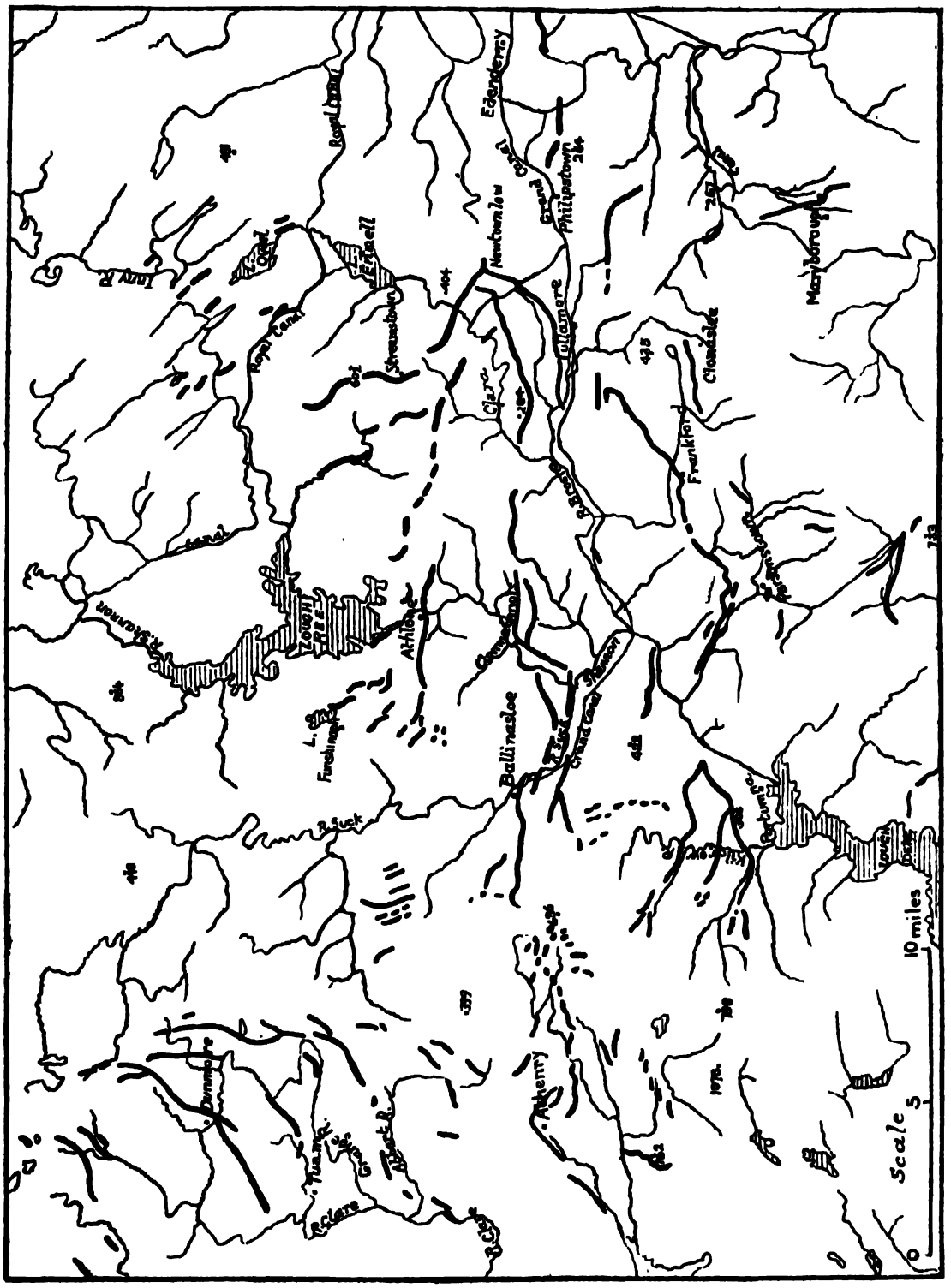



FIG. 1.—Sketch Map of the Irish Esker Systems (mainly after SOLLAS). The three chief convergent series are those of the Clare Basin, near Dunmore, of the Kilcrow River, near Lough Derg, and of the three esker lines which converge towards Newtownlow.

eskers to the south and south-west of Edenderry. From them it is separated by a gap of about eight miles, which might be due to subsequent denudation.

The Ballyduff Esker is exposed in gravel pits beside the roads going north-west and north from Tullamore. The esker begins about 5½ miles west-north-west of Tullamore, and good sections of it are exposed two miles north-west of the town by Ballyduff Bridge (fig. 2). The core of the esker there is a ridge of well bedded sands and fine gravel with a slight dip to the north. Four layers of clay are interbedded in the sands. These beds have been cut through by two faults with a downthrow to the north. These faults were contemporary with the formation of the esker, because the coarse gravel which forms the upper sheet of it passes unbroken across these faults. This fact is fatal, for this esker, to the supraglacial river theory. On the southern side the bedded sands have been denuded, and a coarse torrential gravel occupies the hollow thus formed, and passes upward into a fine-grained bedded gravel, which on each side dips away from the crest of the esker. The sands of the esker core were obviously once much wider, and are the remains of material deposited in quiet water. The faulting was probably produced by subsidences consequent on the melting of masses of ice included in the sands, as after the faults were formed powerful currents of water spread a sheet of coarse gravel over the ridge of sand.

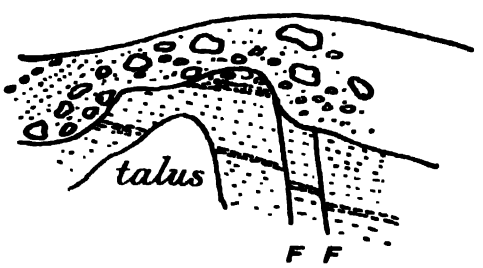



FIG. 2.—Section in an Esker, with contemporary faults. Ballyduff Bridge.

Sections on the southern slope of the esker beside the road to Kilbeggan, 1½ miles north of Tullamore, expose at the base a coarse bouldery wash, which passes laterally to bedded sand and loam containing irregular masses of gravel and steeply inclined shoots of clay. The clay has a very steep dip and appears to have been dumped in its present position by slipping down a steep bank. The upper part of the esker consists of a regularly bedded loam.

The arched structure, which is often described as characteristic of eskers, is absent from this pit and from most of the sections in the Tullamore Eskers. Thus 2 miles north-east of this pit, to the south-east of Derrygolan Bridge (fig. 3), the base of the esker is a bed of stratified gravel with a flat upper surface which has a very slight inclination to the north. This bed is covered by a layer crowded with limestone and chert boulders, which are as much as 15 inches in diameter; they are all fully water worn, and lie horizontally. Some of the layers in this bouldery wash consist of closely packed cobbles and pebbles, and contain but little sand. The bedding

planes are cut off abruptly by the slopes of the esker (fig. 3), which is therefore the remnant of a once wider ridge.



Fig. 3.—Section of an Esker, with horizontal bedding. Derrygolan Bridge.

Deeper sections in the same esker are exposed a mile further to the north-east at Murphy's Bridge The base of the esker there is a bed of sharp sand containing some well rounded grains. The upper part is a bed of stratified dark to greenish sand and gravel, which contains a few small boulders and dips regularly to the north. This bed and its bedding planes are abruptly cut off above by from three to five feet of coarse bouldery gravel, which forms the surface of the esker (fig. 4).

Near Newmill Bridge, a mile further north-east, are some excellent sections in the part of the esker sketched by Du Noyer (figs. 9 and 10, 'Mem. Geol. Surv., Ireland,' Explanation Sheet 98, etc., pp. 30–31). Three large adjacent pits show striking variations in the material. The south-western pit beside the old limekiln is characterised by its regular bedding. The base is a coarse wash with boulders a foot in diameter; above this is a layer of well bedded loam and clay, which is covered by a bed of sand containing large boulders. This is covered by a layer from 2 feet to 6 feet thick, which is crowded with boulders up to 2½ feet in diameter. At the top of the esker is a bed of gravel 10 feet thick, with inconspicuous bedding and boulders up to a foot in diameter. The planes between the successive beds are cut off abruptly by the southern slope of the esker, showing that the beds were once more extensive.

Immediately to the north of this pit, on the opposite face of the esker, is a pit in sand with very confused false bedding. It offers a striking contrast to the regular bedding and coarse boulders and gravel of the southern pit.

The third pit, the north-eastern, is a confused mass of bouldery wash. The only evidence of stratification is afforded by occasional horizontal patches of large boulders. Some of the boulders are standing on end. The material in this pit, owing to the size and arrangement of the boulders, is very morainic in aspect; it resembles the redeposited moraine stuff of some of the larger Swiss moraines.

A little further to the north-east the esker turns abruptly north-west and is continued as the Newtownlow Esker and Long Hill. Good sections are exposed at Newtownlow. The base of the esker consists of coarse gravel, including patches of bouldery wash. Above this gravel is a thick bed crowded with large boulders, and against its steep western margin the bedding planes in the gravel have been inverted. This disturbance was contemporary (fig. 5); for this boulder bed and the gravels beside it have been planed off and a layer of sand is continuous across the

junction. This sand is covered by bouldery wash which usually forms the surface of the esker.

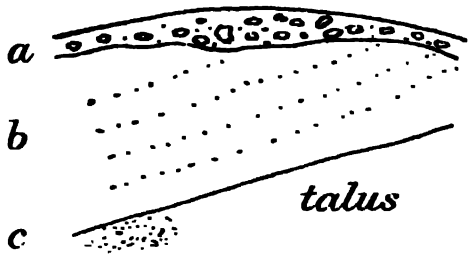



Fig. 4.

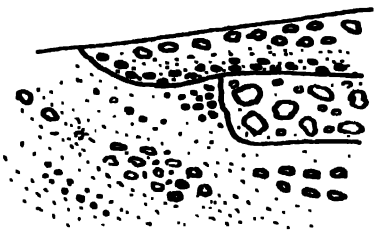


Fig. 5.

Fig. 4.—Section in an Esker at Murphy's Bridge, with fine sand near the core and coarse boulder drift on the top.

Fig. 5.—Section in an Esker, showing great contemporary erosion. Newtownlow.

Three miles west of Newtownlow, to the south and south-west of the village of Kilbeggan, is a long low esker parallel to the Long Hill Esker. It lies on the floor of the area included within the horse-shoe course of the Newtownlow, Ballyduff and Clara Eskers. Some shallow sections in the gravel pit near the fork of the road half-a-mile south of Kilbeggan show the general character of the material. The western end of the pit consists of beds of sharp sand separated by gravel, in which the pebbles and the few boulders present are all well rounded. The aspect of this material is like that of a river gravel. Eighty yards along the pit is a section of stratified sand and fine gravel passing up to gravel with some boulders. At the eastern end of the pit is the following section in descending order.

Soil: 5 feet of unsorted boulder drift; 2 inches of sand; 4 inches fine chert gravel; 18 inches stony loam, including 12-inch boulders; 1 inch to 10 inches irregular layer of sharp sand; 1 inch to 12 inches loam with very few pebbles; 2 feet stratified gravel, part of a lens which is 25 feet long and 3 feet at its thickest; 18 inches stratified sand with pebbles.

The general character of the Ballyduff-Newtownlow Esker is inconsistent with the glacial river theory. The extreme difference between adjacent parts of the esker, as shown at the three pits near Newmill Bridge, indicate that its material had been brought from the side and not carried along the esker. Its original formation can best be explained by the accumulation of material washed from the adjacent front of a melting ice sheet. The esker is not, however, a moraine, as its thoroughly water-worn character and bedding show that it was deposited by sheets of water. The material had obviously not been carried far by water, and its lateral variations are dependent on the nature of the drainage from the ice front. The material in the north-eastern pit at Newmill Bridge probably accumulated where the ice front was a steep wall, at the foot of which the boulders collected in heaps. The false bedded sand of the middle pit was deposited where a stream flowed from the ice. The wide-

spread horizontal sheets of alternate sand and gravel in the south-western pit were doubtless due to variable floods of water.

The composition and structure of the Ballyduff-Newtownlow Esker, therefore, indicate that it was a marginal formation produced by the wash of material from a receding ice front; and this explanation agrees also with the general plan of that esker system.

The distribution and levels of the Parsonstown, Clara and Streamstown Eskers show that they are marginal formations beside an ice sheet which came from the north-west down the Suck and Shannon Valleys.

The Kilbeggan Esker, on the other hand, is like the Swedish osar, fluviatile in character and was probably deposited as a delta formation at the receding mouth of a glacial river.

### 2. *The Athlone Esker.*

South of the railway to the west of Athlone a large pit exposes a high section of a very coarse stratified gravel containing in one part closely crowded boulders up to 2½ feet in diameter. Owing to the size and number of these boulders the material looks more morainic than fluvio-glacial. All the material has, however, been water washed, and the boulders were probably rolled from the ice down a steep bank of pebbles, so that they were easily moved a little distance from the actual edge of the ice.

This morainic type of esker continues west of Athlone and is well exposed near Mount William, about 1½ miles west of Athlone, in the large ballast pit north of the railway. The pit illustrates the variable structure of this esker. The south-eastern part is strewn with big boulders, up to 6 feet in diameter; some of them show glacial striæ of the curved, blunt, short type, like those formed by the twisting movement when stranded ice is swung by the tide. The south-western corner of the pit is in a thick deposit of well bedded sands, which are in places false-bedded and contain some pebbly layers. At the north-western part is a projecting mass of coarse-grained angular faceted gravel, which has been cemented to a hard conglomerate, while the interbedded soft material has been worn into caves. The eastern part of the northern face of the pit exposes a variable series of boulder drifts, gravels, sands, and loam; the upper layer is usually a boulder drift overlying sand, with puckered and faulted seams of clay. In part of this face the beds have been violently disturbed. Towards the eastern end the beds have a dip of 25°, and there are three definite boulder beds inter-stratified with coarse bedded sands.

The beds in this pit include morainic drift along the southern side, sheets of sand which had been deposited in comparatively quiet water, and alternate beds of boulder bearing gravel and sand.

The Athlone Esker is of the marginal morainic type; but the smaller eskers which trend north-westward from it have a well developed banding. Thus about a mile to the west of the Mount William pit in a small pit a little east of Millbrook, the upper-

most bed is a 3 foot layer of coarse drift containing boulders up to 18 inches in diameter; below is a layer of coarse sand, and then another 3 feet of bouldery drift containing boulders 20 inches by 30 inches. The stones in both gravels are water worn, and many of the pebbles are as rounded as in a river gravel. I saw in this pit no trace of glacial striæ. The banding shows variations in the rate of deposition, but there is no evidence to show whether it was due to seasonal changes.

Two miles further to the west-north-west, beside the junction of two roads, just south-east of Ballymullakill, is a large gravel pit, the face of which is partly overgrown, and the relations of the beds in places obscured by slipping. The pit, however, gives evidence of frequent alternate increase and decrease in the currents by which these deposits were laid down. In the length of 85 yards occur seven bands each composed of small boulders, cobbles, and coarse gravel; these bands are separated by layers of sand with small cobbles and pebbles. These bands dip to the north. At the southern end of the pit is a bed of gravel with a steep eastward dip; it has been cut across by a channel filled with boulder drift.

The banded structure of the esker is also shown a little further along it in a pit to the north of the road, half-a-mile west of Ballymullakill and a mile and a quarter south-east of Brideswell. Parts of this pit are overgrown; but the section shows, in a length of 100 yards, eight beds of bouldery drift which are separated by beds of sand and fine gravel (figs. 6 and 7). The beds dip to the north.

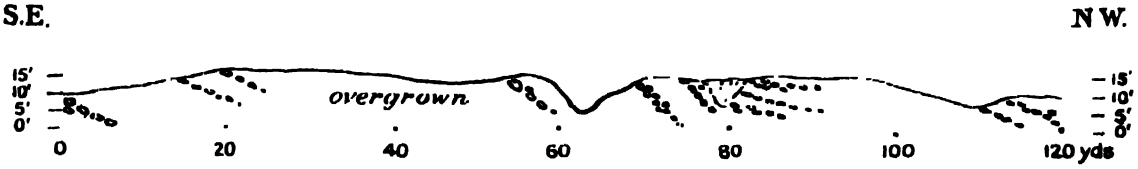



FIG. 6.—Longitudinal Section in the osar at Ballymullakill, north west of Athlone, showing the repeated beds of coarse bouldery gravel. Heights in feet; lengths in yards.

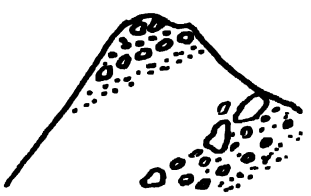


FIG. 7.—Section in the osar north-west of Athlone.

These and other pits between Athlone and Lough Funshinagh give clear evidence that this esker was formed by a stream flowing south-eastward, and that the banded structure was due to the varying strength of the current. It is tempting to regard the variation as seasonal, the succession of coarse to fine material representing the variation during one summer's melting. This banded structure is, however, so irregularly developed that it would be unsafe to conclude that the successive bands represent deposition in succeeding years.

The character of this banding could best be determined in the winter, when the coarse bands of material could be recognised beneath the turf. Detailed mapping of some of these longitudinal eskers would probably determine whether their banding is a seasonal stratification.

The Athlone Esker breaks up westward into a series of irregular mounds and short ridges, which are well developed around Castlesampson. Eastward it passes Moate, and probably continues as the ridge thence northward and north-westward along the valley of the Tang River, a tributary of the Inny, to the south-east of Ballymahon.

The Athlone Esker appears to have been formed by a glacier which came down the Shannon valley and through Lough Ree. It was bounded on both sides by driftless highland—to the west by that, over 500 feet high, south of Roscommon and east of the Suck valley; to the east by that south-east of Longford and that, over 400 feet high, east of Lough Sunderlin and Ballymore.

### 3. *The Ballinasloe-Clonmachnois-Clara-Streamstown Esker.*

To the south of the Athlone Esker is one of the longest, most regular, and best developed eskers in Ireland. It begins about eight miles west of Ballinasloe; its general course is from west to east, though it makes successive curves southward through Ballinasloe, New Town, and Cornaveagh. It is there breached by the Shannon, on the eastern bank of which, at Creevagh, it is joined by a branch which passes south of Ballinasloe through Glenlougham, Kellysgrove, and Shannon Bridge. The combined esker runs from Creevagh to Clonmachnois, where it again subdivides; the northern branch is the Pilgrims' Road Esker, and the southern branch continues due east through Clonfinlough and Togher, and, after a gap made by the valley of the Brosna, to Clara. It passes Durrow, south of Kilbeggan, unites with the Ballyduff-Newtownlow Esker, and bends sharply back and forms the narrow ridge known as the Long Hill; it crosses the Brosna valley, continues further north as the well known Streamstown Esker, and ends in the esker near Moyvore.

This esker is about 65 miles in length from its western end near Woodlawn, on the watershed between the Shannon and the Dooyertha (a stream entering Galway Bay), to its north-eastern end in the Inny valley; it is not, however, continuous for the whole distance. The esker receives a series of branches, and affords one of the best Irish examples of an esker with confluent tributaries, such as suggested the formation of eskers by rivers in glacial canyons. If that had been its origin, the combined river would have been formed by three main streams. The north-eastern stream would have deposited the Long Hill of Newtownlow, and would have been joined by tributaries from Streamstown, Ballymahon, and Athlone. The second main stream would have come from Ballinasloe, Clonmachnois, and Clara; and its chief tributary would have been that of the Shannon Bridge Esker. The most southern of the three main streams would have come from Tullamore and have carried the drainage from

Parsonstown, Eyrecourt, and Portumna. The outlet of the three combined rivers would have been past the fragmentary eskers south of Edenderry.

I have examined this esker at a good many localities and failed to find that its structure agrees with the glacial river hypothesis. The shape of the boulders is not that typical of river gravels. In most places glaciated stones can be found, whereas the striæ disappear after transport by water for a very short distance. Even when no striæ are observable the boulders and pebbles commonly have flattened surfaces, characteristic of those of boulder clay. In some bands of gravel the stones have all been washed and rounded; but these bands form a small proportion of the constituents of the esker, and the abrasion of their stones and removal of the striæ may have been by surf action or by small local streams. The deposits are often unbedded or show only very faint and obscure traces of bedding. In some pits the material appears to have been merely dumped where it lies. The boulders may be packed very closely and large boulders often stand upon their ends. The aspect of many pits is morainic, and they include layers of sand or clay deposited on the floors of depressions in the drifts.

This esker and its branches appear to have been formed on the margin of an ice sheet, which came from the high grounds to the north-west in Mayo and eastern Galway, and deposited ridges of drift at various stages in its retreat. The branching of the esker appears to be due to the ice margin having remained stationary at one place, while it receded in a neighbouring locality. Thus the glacier held its position near Newtownlow while the ice front in the Shannon valley receded about 15 miles.

The evidence for these conclusions may be summarised as follows:—

*The Ballinasloe Eskers.*—West of Ballinasloe the esker is well exposed in pits beside the railway near Kilmalaw Bridge, north of Aughrim. The esker there consists of a confused mass of closely packed boulders, which are especially numerous in the top layer. Rough bedding can be seen in some layers. The largest boulder observed in the pit at Kilmalaw Bridge was 2½ feet long. The boulders are often ice-scratched. Half a mile to the east of the Kilmalaw pit is another gravel pit of the same type. The bedding is obscure and the material appears to have been dumped. The boulders are irregularly packed.

Between 1½ and 3 miles west of Ballinasloe, to the north of the railway line, is the Kilcloony branch of this esker. It is well stratified and consists largely of alternations of boulder drift and gravel, with some layers of sand. A pit south of the road about halfway along this esker shows a 6-foot bed of closely packed boulders, some of which are vertical. Beneath the bouldery drift is a bedded, fine-grained gravel. The structure of the eastern end of the Kilcloony Esker is well shown in two pits to the west of the lane leading to the church. The southern pit includes two beds of bouldery drift, separated by 10 feet of gravel. The beds have a steep dip to the north. In the northern pit the gravels are covered by 3 feet of false-bedded sand with lenticles of well-washed gravel; but in a layer of coarse gravel immediately

beneath the sand are many well ice-scratched stones. The gravels include pebbles of a fine-grained gray biotite-granite and foliated granites which doubtless came from western Galway. The chief deposits of sand in these pits occur, as usual, on the northern side of the esker, as if they had collected in water between the esker and the receding ice front.

Half a mile south-east of Ballinasloe, on the western side of the canal just north-west of Somers Villa, is a gravel pit in the main Ballinasloe Esker. The core of the esker consists of a coarse bouldery drift with some interstratified beds of subangular gravel. It is capped by bedded sand and fine angular gravel which, on both sides of the esker, have been faulted. After the formation of these faults a layer of coarse pebbly drift was deposited across the esker, so that the faulting was clearly contemporaneous with its deposition. A bed of sand occurs on the northern slope of the esker. Some of the boulders are striated, and after the striation were encrusted by calcareous layers, one of which Madame LEMOINE has identified as a Lithothamnium. This esker rests on boulder clay, which is exposed in a pit beside the towing path of the canal, and the upper part of this boulder clay contains boulders bearing marine encrustations showing algal structure.

The Shannon Bridge branch of the Ballinasloe Esker is well shown in a pit 2½ miles south-south-west of Ballinasloe, near Kellysgrove, and in other pits near Sinclair's Village and by Glenlougham Church. A section across this esker at Kellysgrove was figured in the 'Geological Survey Memoir' (Sheets 96, 97, etc., 1867, p. 25), and shows that the stratification is not in the same direction as the outer slopes. The bedding is arranged as a trough and not as an arch.

A pit just north-west of Sinclair's Village shows the close packing of the boulders which sometimes occurs in this esker. The boulders lie at all angles; they are not striated. Their matrix consists of narrow partings of a coarse sand, which includes some cobbles and small boulders. The largest boulder in the area sketched was 4 feet long by 1½ feet thick, and a 6-foot boulder lay on the floor of the pit. A few of the pebbles are of porphyritic granite. The aspect of this pit (see fig. 8) is that of a moraine with closely crowded boulders.




FIG. 8.—Part of Face in a Pit N.W. of Sinclair's Village, near Ballinasloe, showing crowded boulders. Scale, 1 inch = 5 feet Boulder *a* is 4 feet × 1½ feet; boulder *b* is 3 feet 8 ins. × 1 foot 10 ins.

*Kellysgrove Esker.*—At Glenlougham, to the west of Kellysgrove, the core of the esker consists of false-bedded gravel, with boulders and patches of sand. The sand

patches consist of irregularly deposited lenticles. The upper part of the pit is in roughly bedded bouldery drift of morainic aspect. On the south side this bouldery drift is intercalated with wedges of gravel and coarse cobbly gravel. A short search yielded in the gravel six specimens of Galway granite.

*Shannon Bridge Esker.*—The Kellysgrove Esker is a continuation of the Shannon Bridge Esker, the structure of which is well exposed in pits south of the Ballinasloe road, west of Shannon Bridge. A long, shallow section on the northern face of the esker shows a crowded medley of boulders which are up to 2½ feet in length; this bed overlies a black chert sand, with a steep dip to the north. The esker contains a few thin layers of clay. The deeper pits on the southern side show an unwashed, unsorted material, which is arranged as a confused dump. The structure of the esker agrees with its origin as a morainic deposit.

East of Shannon Bridge the esker bends to the north-east, and follows the eastern bank of the Shannon until it joins the Ballinasloe Esker near Clonmachnois. At Cloneff, south of the junction with the Ballinasloe Esker, the Shannon Bridge Esker consists mainly of sharp, angular, bedded sand, with lines of water-washed pebbles. This material would pass as fluvioglacial, but the sections are small and obscure. The nature of the esker must be judged by its characters where better exposed.

A little further north, to the west of Lough Nanag, the esker branches, and encloses a series of pits and hollows shown in the detailed map and sketches published in the 'Geological Survey Memoir' (Sheet 98, etc., pp. 24, 25, 26). A pit to the west of the road shows coarse bouldery drift overlying a bed of ill-sorted water-worn gravel; the boulders lie at all angles; some are vertical, and occur in a coarse pebbly sand.

*Clonmachnois.*—Just east of the Seven Churches at Clonmachnois, three-sixteenths of a mile east of the school, some shallow excavations show an irregularly dumped cobble gravel with faceted boulders, on which I did not see any striæ, and irregular patches of loam. There is no sign of deposition by streams of water. The material appears to have been dropped irregularly in water.

From Clonmachnois, two branches of the esker continue eastward; the northern branch is that of the Pilgrims' Road. The southern branch goes easterly, and extends, though with one gap of nearly four miles, to Clara, around which are many large and instructive sections.

*Clara.*—North of Clara Church are some deep pits in drift resting against a plateau. The lower part of the drift consists of false-bedded sand and gravel, with a prevalent dip to the east. The upper part is a bed of bouldery drift, 20 feet in thickness, which contains irregular patches of sand and fine gravel. The upper bed has in places been cemented to a conglomerate, which overhangs the underlying gravel. In the eastern part of this line of pits the gravels are covered by laminated false-bedded sand and pebbly gravels, with occasional boulders; these beds are in places faulted, and include large pockets of bouldery drift.

The material in these pits is described in the 'Memoir of the Irish Geological Survey' (Sheet 98, etc., pp. 28 and 29) as an esker; but it is admittedly not an isolated ridge, for the beds flank a Carboniferous Limestone plateau, part of which is driftless. This material was apparently deposited where an ice sheet from the north-west melted against the side of the plateau. Some of the material was washed and sorted, and patches of sand collected in the depressions. The beds have been faulted and disturbed by slips during the settlement of the material.

East of Clara the Clonmachnois Esker subdivides. The southern branch is followed by the Tullamore road for a couple of miles, and then bends northward, reuniting with the northern branch near Durrow Abbey. The northern branch crosses the Brosna River, and then turns south-south-east, forming a ridge, which occasions the remarkable meander of the Brosna about a mile and a half east of Clara. Between the two branches of the esker the land is level and low.

The structure of the two branches of the Clara Esker may be illustrated by reference to the sections at the pit at Lehinch, and by the large gravel pits at Ashfield, $1\frac{7}{8}$ miles from Clara, on the road to Tullamore. The Lehinch pit is of interest, on account of the occurrence of a band crowded with fragments of minute calcareous tubes, some of which grow in tufts. The pit is on the eastern side of the road leading to the bridge over the Brosna, at the end of its horseshoe loop. The core of the esker at this point consists of sand and fine gravel, which are arranged in a shallow trough. At the west-south-west end the sands and gravel dip 50° to the south-west. This material is abruptly cut off above, and is covered by a bed of gravel composed of rounded and angular cobbles. Similar material covers the middle of the esker, and, on the other side, slopes down to the east-north-east. It is there covered by a bed of laminated sand and fine gravel, which dips 20° to the east-north-east. This material has the characteristics of an angular beach gravel. It is 10 feet thick. Below it is a layer, 1 foot in thickness, of coarse, loosely packed boulders, the largest of which are about 10 inches in diameter. In the sand between these boulders are many joints, and occasional tufts of calcareous tubuli. Many of the stones in this layer are encrusted by calcareous tubuli. Beneath this bed is a 9-inch layer of fine-grained gravel, also containing encrusted stones. Below are 18 inches of an angular beach gravel; it rests on a 6-inch boulder bed, in which the boulders are encrusted by tubes.

The Ashfield pit, on the southern branch of the Clara Esker, is better known, as it is larger, and is situated beside the high road to Tullamore. The core of the esker consists of a bedded gravel with an arched dip. The ridge is not symmetrical in section. The beds dipping south, on the southern side of the esker, are much thicker than those on the northern side, which dip north. The stratification on the northern side is more confused and irregular. The bedded gravels, which form the main mass of the esker, are covered by a bed crowded with boulders.

After the reunion of the two arms of the Clara Esker, it passes Durrow Abbey to

Newtonlow, where it bends sharply back to form the Long Hill, which is cut through by the Brosna River south of Ballynagore, and is continued, though with two gaps, through the eskers of Streamstown and Moyvore to the Inny Valley.

### 4. *The Athenry Esker.*

West of Ballinasloe the eskers are represented by irregular patches and mounds of drift.* Near Athenry the esker is again developed in continuous ridges, one of which is well seen from the railway to the north of Athenry Station. The structure of this esker is well exposed where it is cut through by the Tuam Railway, and in pits and road sections thence westward past Athenry toward Castle Lambert.

The section at the Tuam Railway shows the following section in descending order :— Bouldery drift, inclined southward, 10 feet; fine-grained, black chert gravel containing numerous boulders; this gravel occurs in three layers, two of which unite in the middle of the section; the two bouldery beds there end off against a tumbled mass of boulders, which form the core of the esker. On both sides the beds dip away from the middle line of the esker. Some of the boulders are striated.

A small road section to the west of this pit shows a well-defined repetition of the coarser bands, to which my attention was called by Mr. R. Durdle; and, as he remarked, this structure seems too indefinite to be a seasonal banding, though it is clearly due to variations in the strength of the currents which distributed the esker material.

On the southern slope of the esker, a little west of the last section, is a small pit, 10 feet deep, in a well-bedded coarse gravel interbedded with a much finer gravel. At the eastern end there are five layers of coarse gravel with cobbles; at the western end these have united to form only three layers. Some of the boulders in this pit are as distinctly glaciated as those in boulder clay.

At a pit further west, on the eastern side of the Tuam road, are numerous patches of sand in boulder drift. The arrangement of the material in this pit is very irregular, and the sheets of sand were probably deposited in water between the ice front and the esker.

At the quarry a little further north on the opposite side of the Tuam road the surface of the limestone is well glaciated. Upon this rests a sandy drift containing many striated and encrusted boulders. This material is identical with that sometimes described as boulder clay, though it is so sandy that the term clay for it is a misnomer. This drift does not at the quarry give rise to esker forms, though some of the sections are indistinguishable from esker drift; thus, in one place, a bed of false-bedded sand and gravel is cut off above, and is covered by a coarse morainic bouldery drift. The largest stones in this drift are striated.

The Athenry Esker in the sections from the Tuam road eastward to the Tuam

* 'Mem. Geol. Surv., Ireland,' Explanation Sheets 96–7, 106–7, p. 28 (1867).

railway is largely composed of sand and fine gravel. The sand is often as sharp as sea sand, and it is capped and interbedded with boulder drift.

### 5. *The Ballyhaunis and Dunmore System.*

One of the best cases of several eskers joining like the confluent tributaries of a river is supplied by the Ballyhaunis system. Thus in the Tuam district three eskers, which trend north-eastward, unite near Ballinlough (fig. 9).

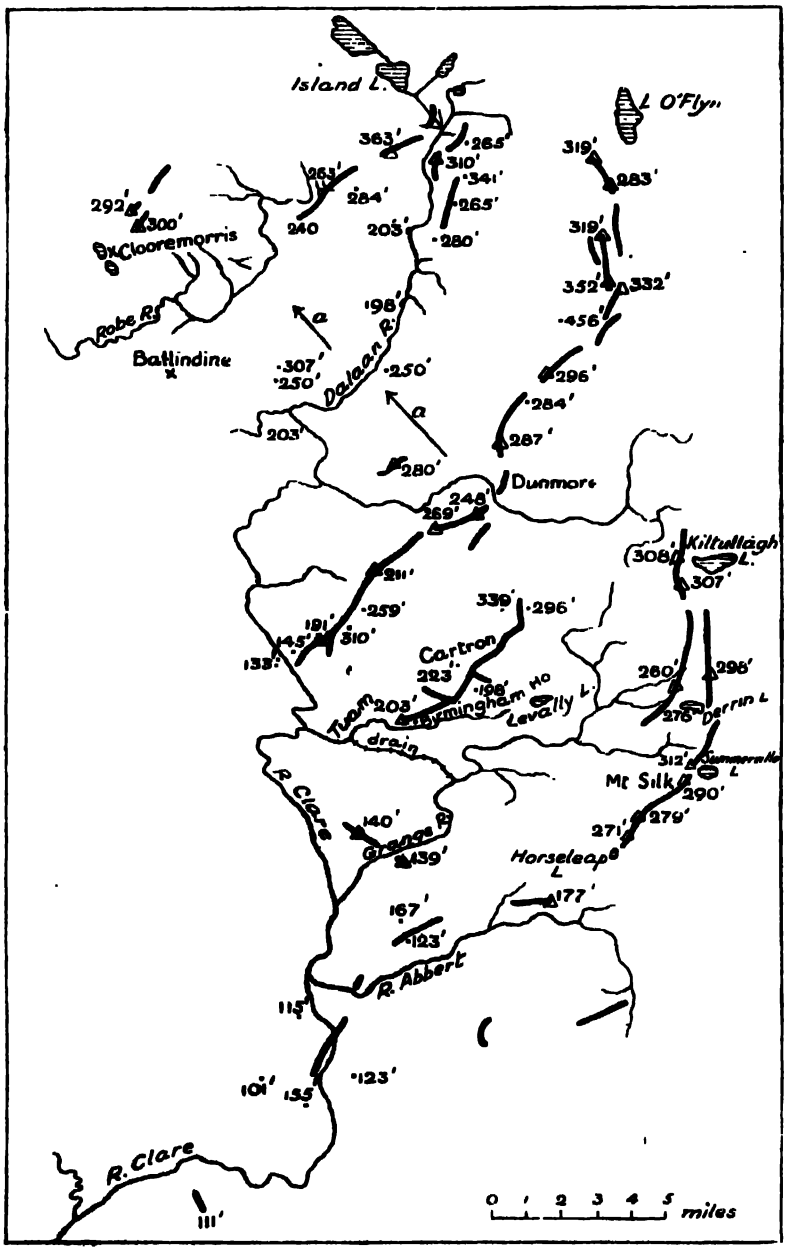



FIG. 9.—The Esker System, near Dunmore, Co. Galway. The arrows, *a*, *a*, show the course of the ice movement (after SOLLAS). Heights in feet from Ordnance and Geological Survey Maps. The eskers in this system are transverse to the course of the ice movement; they approach one another to the north, where the levels are higher than to the south. Eskers shown by thick lines. *For* Clooremorris *read* Claremorris.

Of these three eskers the southernmost follows at first the course of the Abbert River, and then crosses the divide between it and the Grange River, passing about six miles south and south-east of Tuam through Ballyglunin and Mt. Silk; it bends first northward through Raheen to the west of Kilnalag, and then north-westward to join the second member of this system.

The second esker begins a little east of Tuam, 2 miles east of which it passes Birmingham House; it is well developed 2 miles further east about Cartron; thence it trends north-eastward, and, after a long gap near Lake Makeeran, continues north through Stoneypark, and west of Cashel and Kilnalag, where it joins the two other eskers. The branching of this esker near Stoneypark is described and illustrated in the 'Mem. Geol. Surv., Ireland,' 1871, Explanation Sheets 86–88.

The third branch starts 2 miles north-west of Tuam, passes through Castletown and Dunmore, and joins the other two eskers, which continue northward towards Lough O'Flyn.

The easternmost of these three eskers lies along the watershed between the Clara and Suck Rivers. The general level of the adjacent country rises from south and south-west to north and north-east. As the ground is sloping southward if the eskers had been due to three rivers which had cut channels through a glacier down to the underlying rock, their flow should have been southward, and not in the opposite direction. On the fluviatile theory the rivers would have been divergent from the north and north-east, rather than confluent from the south-west. The three eskers, moreover, lie across the main direction of the ice flow. The distribution of the erratics, the directions of the striæ, and the trend of the drumlins, show that the main flow of the ice was from north-west to south-east.* These eskers were probably deposited along the edge of the ice sheet at stages in its retreat.

The morainic character of these eskers is shown in sections near Castletown House to the south-west of Dunmore, at Pollaphuca, at the old lime kilns beside the road junction to the south-east of Knockavenny House, and along the main road to Tuam near Birmingham House. The structure of the Dunmore Esker may be illustrated by reference to six gravel pits north-north-east of Castletown House and between it and the Dunmore road, near Grange. North of Castletown House the esker occurs in three branches, each of which has been cut through by the road. The eastern branch consists of beach material, with patches of fine gravel and scattered boulders, some of which are 2 feet long. It rests upon boulder clay, which is exposed in the low ground to the west. The westernmost division of the esker is very sandy, and is said to have yielded shells; but I did not find any.

The general character of the material in this part of the Dunmore Esker is an unstratified morainic drift. It may be described as a gravelly beach moraine. Most of the sections yielded ice-scratched stones and boulders up to 1 foot long; the

* Prof. Sollas recognised that the eskers near Ballyhaunis, Dunmore, and Tuam lie across the ice flow; he suggested that the position of the esker-forming rivers was determined by crevasses.

largest measured is 4 feet in diameter. The upper layer consists of a bedded sand. One of the best pits is that close by the roadside, south of Grange; in it the boulders range up to 3 feet in diameter, and are mixed with black chert, gravel, and sand; a faintly bedded character is given to the deposits by short lines of sand, but the material, as a whole, is unstratified. The irregular arrangement of the boulders and occasional bedding give this pit a morainic aspect.

The esker near Birmingham House and Pollaphuca shows more clearly the characteristics of a morainic drift, which is either unstratified or but occasionally stratified. It is therefore very different in character from ordinary fluvioglacial material. The pit in the esker just west of Birmingham House, 2 miles east of Tuam, contains boulders 2½ feet in diameter, in coarse unstratified morainic drift.

One and a quarter miles further east, a branch road to the north-east towards Cartron cuts through this esker and shows clear sections, one of which is at an old kiln just by the junction of the two roads. This pit exposes unstratified bouldery drift, cut off above by a level layer of sand resting on a line of cobbles; above this old surface, which is the only definite stratification in the pit, is a layer of boulders and cobbles. The top of this esker must have been planed down and covered by a layer of sand, upon which fresh bouldery drift was deposited.

To the north of the bog, on the road to Cartron, the esker is exposed again on the western side of the road. The most interesting feature in this pit is the presence of large encrusted boulders, some of which are standing on end. Thus, in the upper part of the pit, a boulder, which is 2 feet 8 inches high and 2 feet 4 inches wide, is standing upon its lower edge, which is only 10 inches wide. None of the boulders seen are striated.

These two members of the Ballyhaunis system are therefore not composed of fluvioglacial, but of morainic material. The Ballyhaunis Eskers were probably deposited by ice, which came from the hills of Mayo, as a series of beach moraines at successive stages in its recession to the north-west.

### 6. *The Ross–Gortachalla Esker.*

The Ross–Gortachalla Esker, about ten miles north-west of Galway, extends from near Ross Station eastward to Loch Corrib. It was briefly described by KINAHAN,* and SOLLAS (1896, p. 809) has suggested, as a "bare possibility," that it may belong to the Ballyhaunis system. Its course is irregular, as denudation has in places broken it into isolated mounds. A pit, south of the esker and south-east of the Roman Catholic chapel at Ross, shows that it rests on a sandy boulder clay, which contains many boulders of limestone and some of porphyritic granite. The material in the adjacent esker is a stony gravel, with the pebbles strongly faceted and not very water-worn. Sections north of the road and north of the eastern end of Ross Lake show that the esker there consists mainly of closely packed pebbles,

* 'Mem. Geol. Surv., Ireland,' Explanation Sheet 105, p. 44 (1869).

while the lowest layer exposed is of sand, with but few pebbles. The cobbles are mainly of limestone and chert, with a few of gneiss and schist, but I saw none of the granite, which is so abundant in the boulder clay. The esker here consists of the remains of two ridges, and a third is represented further to the south, on the margin of Ross Lake. A pit in the esker knoll, situated just east of the road which goes south past the eastern end of Ross Lake, exposes a typical glacieluvial gravel, which is unstratified, and has abundant pebbles of schist and gneiss, but I saw none of granite. Many of the pebbles are faceted, but are not striated.

A gravel pit near Ower contains at its northern end many limestone boulders, from 3 to 4 feet in diameter, in a faintly bedded, fine-grained sand. At the southern end of this pit the sand is coarse, sharply angular, and unsorted; it is not a river sand, but resembles a bed of sand formed as rainwash. The arrangement of the materials here suggests the former existence of a lake between the ice and the esker. South of Ower the esker is a high, narrow, irregular ridge, which is steepest to the south. Some shallow gravel pits north-west of Gortachalla Lough work a stony, unsorted glacieluvial gravel, which consists of flat-sided, subangular pebbles. They are not striated; there are no boulders, and no specimens of the coarse porphyritic granite from the hills to the south-west. There are, however, abundant pebbles of gneiss and schist derived from the area to the west and north-west. In the southern slopes of the esker, toward the eastern end of Gortachalla Lough, the stones are in places packed as closely as in a shingle beach.

The material of this Ross–Gortachalla Esker is not fluvioglacial, because it is not a river deposit; most of it is unbedded, and, though its pebbles have been so washed as to have lost any glacial striæ, they are still angular and flat-faced. Bedding and layers of sand are exceptional, though they occur where small lakes or ponds had formed between the esker and the retreating ice. The abundance of pebbles of gneiss and schist show that the material came from the west or north-west, and, if the esker had been due to a glacial river, the pebbles should become smaller to the east. This esker seems to me a ridge of typical glacieluvial materials; its composition, course, and curvature show that it was due to a glacier which flowed south-eastward from the mountains of Connemara. The esker was probably deposited along the edge of the Loch Corrib glacier during one stage of its retreat.

### 7. *The Greenhills Esker, near Dublin.*

The Greenhills Esker, to the south-west of Dublin,* is one of the most accessible in Ireland, and is exposed in numerous extensive sand and gravel pits. I was kindly guided to it on my first visit by Prof. Seymour. Its southern end is on the bank of the Dodder River at Balrothery. It rests in places on water-worn Carboniferous rocks, which are sometimes separated from the esker by a sheet of boulder clay.

* 'Mem. Geol. Surv., Ireland,' Explanation Sheet 112, Dublin, 1903, pp. 50–51, 97–100.

The existence of this clay has been used as an argument for the glacial-canyon theory of eskers. The esker in places shows the arched bedding, which is often claimed as characteristic of true eskers. The material is in places finer-grained on the western slope, while the bedding is steepest on the eastern front. Some of the large lenticles of gravel are coarsest to the south, but the included rocks indicate that the material came from the north or north-west—a fact previously recorded by CARVELL LEWIS (1894, p. 149). Glacial striæ are said to be not uncommon on the stones, and Prof. SEYMOUR and I noticed clear glacial grooves on the boulders in the lower part of the esker.

One of the most conspicuous features in the constitution of this esker is the abundance of laminated clay and loam, as in the deep pit at Airmont.* There the loam had been cut away in steps, and the hollows thus formed occupied by a coarse torrential gravel, which also forms the summit of the esker. The gravel often occurs in lenticular patches interstratified in the clays.

This esker is in some places a single narrow ridge, and in others a broad bank of confused interstratified sand, gravel, and clay. The material does not, as a whole, resemble the deposit in a glacial river, for the amount of clay is far greater than would be expected under such conditions.

The characteristics of this Greenhills Esker suggest that it was deposited as a wide bank of laminated sand and loam on the margin of a sheet of water; that the deposition of the finer materials was interrupted by occasional floods carrying coarse gravel; and that finally the bank was cut into by strong currents which deposited on its flanks and above it sheets of coarse torrential gravel.

The arrangement of the materials in this esker appears to indicate their deposition as a marginal bank along an ice sheet. The rise in level southward, although the material has come from the north, is incompatible with the fluviatile theory, unless the river had flowed over the glacier, and such a position appears irreconcilable with the regular bedding of the materials. If they had been first deposited on the bed of a supra-glacial river and then redeposited by the melting of the underlying ice, the bedding should have been more confused and irregular.

### 8. *The Eskers of Tyrone.*

A series of eskers different in several respects from those of the Central Plain occur on the moorlands of Tyrone on the divide between the Shrule, the upper part of the River Foyle, and Lough Neagh; and between the Sperrin Mountains (2,240 feet) to the north, and the hills to the north of Pomeroy. The eskers have been described in 'Mem. Geol. Surv., Ireland,' Explanation Sheets 26, 1884; 34, 1878; and 35, 1877. Some of these eskers are well exposed at Crockadoo (at the cross roads, 487 feet), at the north-western foot of Craigballyharky (771 feet), along the direct road from

* This locality is named Palatine House in the 1902 edition of Sheet 112.

Cookstown to Omagh, near Drumshambo, especially between Dunnamore Bridge (at 500 feet) and Teebane Bridge, and finally north of Creggan School (600 feet).

The eskers to the south of these hills in the valley between Pomeroy and Carrickmore appear to be much larger; they were referred to as kames by CARVILL LEWIS (1894, p. 115). He stated that the "kames" in this district, near Lough Cam, were the largest he had seen. I have chiefly examined those near the Cookstown-Omagh road, where they consist of coarse sand with many faceted but not striated pebbles. At Drumshambo they are mainly granite and greenstones, and the gravel has all the characteristics of glacieluvial deposits. The arrangement of the eskers is seen from the ridge (at 617 feet) west of Barony Bridge; and they are seen to lie along the northern foot of Evishanoran Mountain (886 feet), which is north by west of Pomeroy. The esker rises up the hill side on a sinuous course. It has obviously been formed as a marginal formation due to a glacier flowing northward and north-westward from the Evishanoran Hills. The esker near Dunnamore was probably similarly due to ice from Slievemore (842 feet). This series of eskers seems to have had a similar origin to the ridge at Polmont, in Linlithgow County, which has been described (GREGORY, 1912 (1), pp. 209–210) as a glacieluvial kame.

## III. PALÆONTOLOGICAL EVIDENCE.

OLDHAM (1844, pp. 61–64, 130–132) has collected records showing that marine shells are widespread in the Irish drifts. KINAHAN found shell fragments in the esker at Maryboro*; their occurrence in the glacial drifts to the height of 1,300 feet at Three Rock Mountain near Carrickmines is well known, and the shells there were numerous and well preserved. OLDHAM records them from various localities near Dublin, including Howth, Bray, Swords (150 feet), and Finglass (200 feet), and ranging to the height of 600 feet above sea-level; in northern Ireland his records include Belfast (106 feet), Londonderry (300 feet), County Sligo (100 to 200 feet); in western Ireland, Tarmon Hill, County Mayo (250 feet); at Naas (380 feet); in an esker near Roscrea, County Tipperary, at 400 feet, "in the very centre of the island" (p. 66); also (*ibid*, p. 131) a *Buccinum undatum* in the gravels at Moate, a locality near Clara traversed by the eastern continuation of the Athlone esker.

According to OLDHAM and KINAHAN'S records marine shells have been found at three significant localities in the chief esker district of Central Ireland.

It has been suggested in conversation that these records are mostly based on shells which were carried inland for food and were dropped in the pits by man. The evidence cannot be so summarily dismissed. KINAHAN and MALLET (in OLDHAM, 1844, p. 131) were not likely to have mistaken modern shells for fossils; and as the shells at 1,300 feet above sea-level on Three Rock Mountain are undoubtedly fossil, there is no reason why marine shells should not occur at lower levels inland.

* 'Mem. Geol. Surv., Ireland,' Sheet 128, p. 30 (1859).

The shells in the esker drifts are, however, rare and fragmentary, as is only natural, since the drifts were no doubt deposited in conditions unfavourable either to the existence or preservation of mollusca. Shell fragments are friable and easily dissolved, and there would be little chance of finding them except in newly exposed material. They would probably occur only in pockets, found occasionally when the gravel pits were being worked more extensively than they are at present. The sections at Maryboro where KINAHAN found his shells are now overgrown, and the newer pits to the north are in material very unfavourable to the preservation of shells.

Although it seems necessary to accept the records it would be unwise to lay much stress on them since the shells may have been *remanié* from the underlying boulder clay. The "glacialoid boulder clay" or "semi-morainic drift" of KINAHAN is doubtless non-marine; but the lower compact boulder clay in which foraminifera are widespread, may be due, like the boulder clays in the Spitsbergen fiords, to glacier ice melting in the sea.

Looking for fossils in the eskers my attention was attracted by some calcareous encrustations in boulders near Clara and Ballinasloe, which were composed of confluent discs with lobed margins like Melobesia. Calcareous crusts are common in the eskers, and are no doubt usually tufaceous and inorganic. But some of them so strikingly resembled the nullipores which encrust the boulders on the Spitsbergen coast, that I had sections cut, and the first showed structures like those of calcareous algæ. I therefore submitted specimens to Prof. F. O. BOWER, who reported them to be "either Melobesia or some Melobesia-like organism." To obtain a more precise identification I submitted them to Dr. A. B. RENDLE and Mr. A. GEPP, of the Natural History Museum, who recommended, in order to secure the most authoritative available opinion on their nature, that they should be sent to Madame LEMOINE, of Paris. She kindly examined the material and identified the section from Ballinasloe as unquestionably a Lithothamnium.

Most of the calcareous encrustations in the eskers are no doubt inorganic, as shown by the fact that in some layers they occur only on the under surfaces; in others they have cemented grains of grit and small stones to the boulders. But Madame LEMOINE'S identification shows that some of these encrustations are algal and marine in origin. Others may have had the same formation, but have been so altered by percolating water that any organic structure has been destroyed.* The encrustations which externally resemble calcareous algæ are restricted to special layers and to the low level eskers. I saw none, for example, in the high level eskers of Tyrone: and though their absence thence might be attributed to those eskers containing little limestone, this is not an adequate explanation, as some of the stones have

* The Melobesia-like aspect of these encrustations is soon destroyed on exposure to the weather. On returning to the pit at Ballinasloe, a few months after my first visit, to collect further specimens, I found the features which had led me to suspect their organic origin had almost entirely disappeared.

tufaceous calcareous encrustations. The algal-like encrustations are absent from the eskers to the north-west of Athlone, which seem to me due to glacial rivers; and also from layers of gravel in the main eskers which appear to have been deposited by streams of water.

The objection that if any of these encrustations were of marine origin, shell fragments would occur with them does not seem conclusive, for reasons stated on pp. 145–146.

The evidence of these encrustations is, however, open to the objection that the specimens may have been derived from the underlying boulder clay, the marine origin of which has been persistently maintained, in spite of the rejection of that view by, at one time, the great majority of British glacial geologists. The boulder clay has been shown by Mr. Joseph Wright to contain widespread indigenous Foraminifera; and it seems very difficult to reject such evidence as to the marine origin of this material. If the boulder clay beneath the eskers be marine, it is possible that boulders encrusted by calcareous algæ were dropped into the eskers while embedded in frozen mud; and when the material thawed the clay would have been washed away, leaving the nullipores uninjured on the boulders. Owing to that possibility, the occurrence of Lithothamnium on the boulders is not conclusive of the marine origin of the eskers themselves.

In addition to the laminar encrustations, there are numerous tubular structures. The best preserved are small calcareous tubular branched tufts, resembling Bryozoa, which occur in hollows between the boulders in the pit east of Clara. The adjacent stones contain many encrusting tubuli, which I suspected to be the rooting fibres of Crisidia. On one of these occurred an expansion, which I sketched in the pit as the gonœcium of a Bryozoa, but this specimen was broken in transport. I showed some of these tubes to Sir Sydney Harmer, F.R.S., but he does not accept them as Bryozoa. I also showed some of them to Prof. J. S. Gemmill, to know what else they might be. Owing to their resemblance to Bryozoa, he submitted them to Mr. Alex. Gray, the most experienced authority on the Bryozoa of the Clyde estuary; he stated that, in his opinion, they are the rooting fibres of Crisidia. In view, however, of Sir Sydney Harmer's rejection of this conclusion, the nature of these tubes must be left uncertain.

Some tubular encrustations on the esker stones have been formed by the deposition of carbonate of lime around roots. Some of those near the surface may have been due to the action of grass roots in recent time, but many of the tubes were clearly contemporary with the formation of the esker, as they are found in the lower layers, which are separated from the surface by beds without these encrustations. Vertical calcareous cylindrical concretions, like those commonly found around grass roots and stems in calcareous dunes, occur occasionally, as, for example, in the Maryboro Esker.

## IV. The Origin and Classification of the Irish Eskers.

The Irish eskers appear to include four different formations: (1) fluvioglacial ridges deposited along the course of glacial rivers; (2 and 3) ridges of fluvioglacial and of glacieluvial materials deposited beside the margin of melting ice sheets; and (4) banks of fluvioglacial material left by the denudation of larger sheets. The most important of the Irish eskers are the marginal formations, while the members of the first of the above four classes are comparatively few and small.

The first test whether the eskers were due to subglacial rivers or were deposited as marginal banks, is the source of the esker materials. These should have travelled along such eskers as were made, like Swedish osar, by subglacial rivers, whereas the materials of the chief Irish eskers were introduced from the side. "Drumlins," says Maxwell Close (1876, p. 211), "always seem to have been formed by something that acted along their length, whereas esker ridges seldom suggest such an idea." The available evidence as to the source of the Irish esker material is scanty, since there are few rocks in the esker district which show the direction of the ice movement. Granites and gneisses are strewn over the Carboniferous rocks near the western margin of the Central Plain and indicate a movement from west to east. But in these cases it may be argued that the rocks have been derived from the underlying boulder clay.

### 1. *The Trend of the Eskers and Direction of the Ice Flow.*

Prof. Sollas' map (1896, p. 805, fig. 2) represents the ice movement in the Dunmore district as from south-east to north-west. It is clear, however, that a little further south the predominant movement of the ice, which deposited the boulder clay and probably also the eskers, was from west to east, as granite from Iar-Connaught is found in the eskers near Athenry, and as Kinahan (Kinahan, 1878, p. 249; also Kinahan and Maxwell Close, 1872, p. 9) has recorded erratics of granite from western Galway scattered over the country and sometimes upon the eskers as far east as Woodlawn and Ballinasloe, and south-eastward at Eyrecourt, Portumna, Birr, and as far as Nenagh to the south-east of Loch Derg. The highlands of eastern Mayo rise to the north-west of Dunmore; hence the last ice movement in the Dunmore district would naturally have been from north-west to south-east.

Whether the ice in that district flowed from or toward the north-west, Maxwell Close and Sollas both represent it as having been at right angles to the trend of the Ballyhaunis, Dunmore, and Tuam Eskers. These ridges of loose drift could only have accumulated across the direction of the glacial movement after the ice had become stagnant. But as Tarr has remarked regarding the stagnant ice sheets of Alaska, the rivers have a very short course upon the ice; he states (Tarr, 1908, p. 97) that "no single case was found where an esker deposit was being made *on* the ice . . . the streams are short; they keep their bottoms fairly clear of *debris*; and

in a short distance they disappear to the bottom of the glacier through moulins. Certainly, under Alaskan conditions, superglacial eskers are impossible."

Apart from the Alaskan analogy the local evidence is against the glacial-canyon theory, even if it be modified by assuming the stagnancy of the ice. For as soon as the water had worked its way to the base of the ice, it would have drained down the slope of the land; whereas the course of the confluent eskers is independent of the slope, and is often in the opposite direction. Thus the eskers between Ballyhaunis, Tuam, and Newton Bellew supply, according to Prof. SOLLAS' maps, one of the best instances of eskers joining like the tributaries of a river system. South of Ballinlough, eskers trending from the south-west at Dunmore, from the south at Curragh, and from the south and south-east past Raheen and Kilnalag, all unite into one main esker. The convergence of these eskers is, however, in the wrong direction, for as shown by the altitudes marked in fig. 9, the levels are lowest at the supposed heads of the glacial streams.

The Castletown Esker begins near the Clare River, 2½ miles north-west of Tuam at about 150 feet; it rises a mile north-eastward to 194 feet. The esker near the Grange River south of Tuam is at the level of 140 feet. The south-eastern member of this series begins north of the upper part of the Abbert River at the line of about 130 feet; the level is 271 feet at Horseleap Lough, 312 feet at Mt. Silk. The northern of these eskers near Kilnalag and Ballyhaunis occur a little above the 350 contour. Prof. SOLLAS remarked that these eskers run against the slope of the ground, and suggested that the apparent convergence to the north should perhaps be interpreted as a divergence southward, the water from the Ballyhaunis district discharging seaward through radial channels. This divergence is normal in deltas and where rivers emerge on to plains. The latter condition cannot be appealed to in this district, since the land slopes, as for example along the Dunmore Esker, about 12 feet in the mile; and the course of the eskers is independent of the relief of the land that had been established before the formation of the eskers. If the divergence be explained as a delta formation, it would imply that the eskers there were formed beside the sea or a large lake.

Hence the most striking apparent case of agreement between the plan of the eskers and that of a river system fails when examined more closely. The convergence of the three esker lines towards Ballinlough may be more probably explained as due to the ice front having retreated more slowly there than along the line from Newton Bellew to Dunmore.

### 2. *The Variability of the Esker Levels.*

The well known variability in the esker levels is illustrated in fig. 10 for the esker system from north of Portumna to the Clara district. The Kilcrow River, which enters the north-western corner of Loch Derg, cuts through three eskers, viz., those near Killimor, at Mootbridge, and Newbridge. These three eskers unite before reaching

the Shannon. The northern or Killimor member of this esker series begins at the height of just below 300 feet, and descends to 174 feet where it is breached by the Kilcrow River. It then rises to 222 feet and 235 feet, and descends to 167 feet (with its base at about 150 feet) to the west of the Shannon. The Mootbridge Esker begins at 200 feet; it falls to 136 feet at Mootbridge, and rises to 198 feet at its junction with the third member of the series.

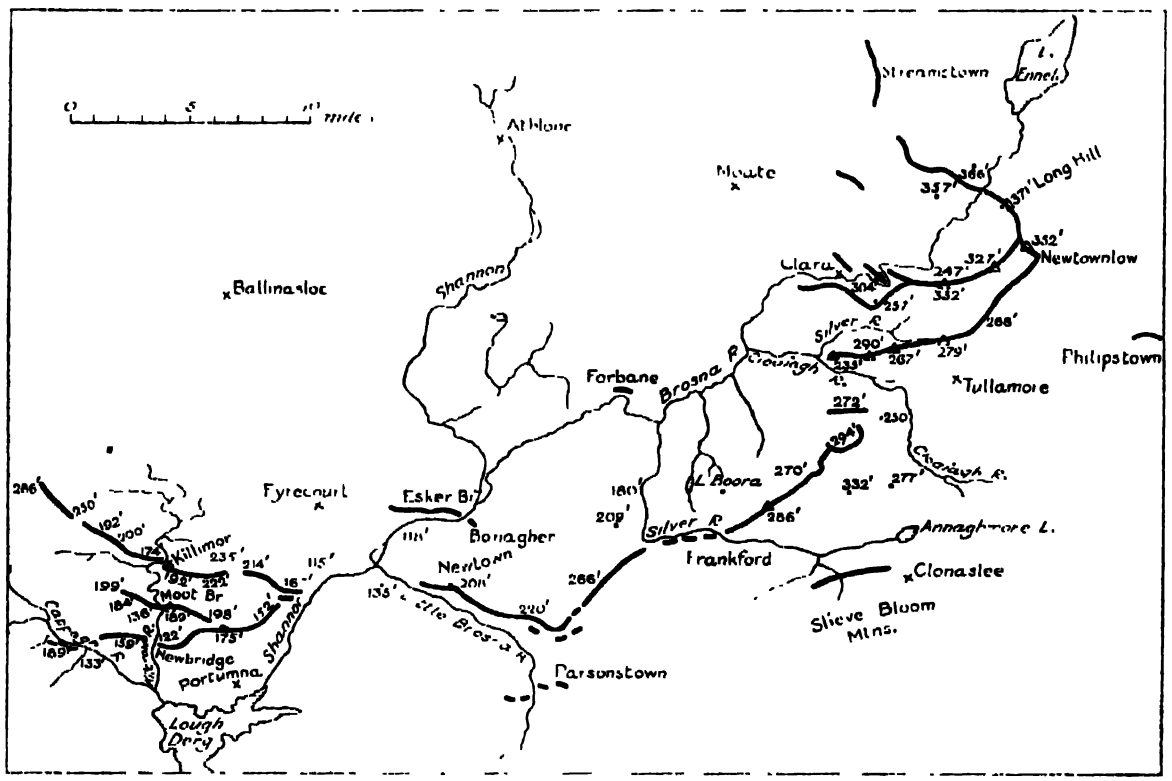



FIG. 10.—The Eskers from Portumna to Newtownlow, showing the rise and fall along their course. Heights in feet.

The Newbridge Esker also begins at about 200 feet, is at 159 feet just west of Newbridge, rises to 175 feet at its junction with the Mootbridge Esker, falls to 152 feet, and rises to 167 feet at its confluence with the Killimor Esker.

On the river theory these three eskers would have been formed by the head streams of the river which deposited the line of eskers from Parsonstown to Tullamore. That esker begins east of the Shannon, at Newtown, north of the Little Brosna River, at about 200 feet; it rises gradually eastward to 220 feet north of Parsonstown, to 266 feet at Fivealley; it is a little lower north of Frankford, and rises again at 2½ miles to the north-east, to 286 feet; 4 miles further north-east it attains the level of 294 feet, and then descends the left bank of the Clodiagh River. It resumes its course at 235 feet in the angle between the Clodiagh and Silver rivers, rises eastward to 290 feet, varies from that level to 260 feet north of

Tullamore, and rises to 352 feet at its eastern bend near Newtownlow as it approaches the eskers from Clara and Streamstown.

Of the two branches of the Clara Esker one begins at 284 feet and the other at 259 feet; the esker rises eastward to 302 feet and 327 feet. The Streamstown Esker occurs at about 350 feet; its continuation south-eastward falls to 326 feet near the Brosna, after crossing which it rises to 371 feet and 368 feet as it approaches the eskers from Parsonstown and Tullamore. The supposed outlet of the esker river from the Portumna district is, therefore, about 200 feet above the level of its head streams. This argument would not be fatal to the theory of the eskers having been formed by superglacial rivers, but that view appears to have no supporters for Irish eskers. As Prof. Sollas (1896, p. 819) observed, the structure of the Irish eskers shows that they were deposited where they are now found, and that they were not precipitated in mass by the sinking of the floor of a glacial canyon. Mr. W. B. Wright (1914, p. 39) remarks that the bedding is "frequently quite undisturbed." The levels are inconsistent with the river theory as advocated for Ireland, for if the canyons had been cut through the ice to the ground, the rivers could not have flowed in an opposite direction to the slope of the land.

It has been pointed out, as by Newberry (1878, p. 41), that some of the American eskers occupy "a topographical position, which makes it impossible that they should ever have been the beds of rivers," as they cross or even lie along the divides. The fact that the Irish eskers are independent of the slope of the country is fatal to the view that they were deposited in rivers flowing through open glacial canyons.

Observed variations in level would, on the other hand, naturally occur in marginal deposits along the edge of an ice sheet resting on an undulating surface.

### 3. *Esker Structures not Fluviatile.*

That the river drift theory does not explain all, or even most, of the Irish eskers is shown by their structures. Glacial rivers, such as those assumed for the formation of eskers, are naturally shallow and rapid; and in them the coarsest material should collect in the centre of the channel, while fine silts would be deposited only in the quieter water beside the banks; but in many Irish eskers the reverse is the case. Thus the core of the Ballyduff Esker consists of fine silt and clay, which is flanked and capped by coarse gravel.

Hershey (1897, p. 242) remarked that in the Illinois eskers the "beds of coarse gravel, cobbles, and small boulders are almost invariably at the top of the deposit, contrary to what we usually find in the product of ordinary stream action"; and the same objection to the fluviatile theory is applicable to many parts of the Irish eskers.

### 4. *The Ridge Form and the Esker Formation in Water.*

The glacial-canyon theory has the recommendation that it offers an explanation of the deposition of the esker material in long, narrow, sinuous ridges. It is true that

these ridges were once wider, for where the grain of the esker is cut off abruptly by the slope (as in figs. 3 and 4), the esker has been reduced in width since its formation. Nevertheless the ridge form was clearly one of the original characteristics of the typical esker. Their composition and structure both show that they are not ordinary moraines. They have been described as "gravelly moraines" (*e.g.*, JAS. GEIKIE, 1905, p. 312); but it seems advisable to restrict the term moraine to direct deposits from ice, and to exclude those in which material derived from ice has been carried and deposited by water. Eskers consist sometimes of fluvioglacial deposits, due to the action of glacial rivers, and of glacieluvial deposits (GREGORY, 1912, p. 210), which are due to the irregular wash of water along the edge of a melting ice sheet. The eskers, according to this nomenclature, are mainly fluvioglacial; and they are usually laid down as long banks of water-worn gravel and sand. Eskers are unknown around Alpine glaciers, and the most similar structures around Arctic glaciers occur where the ice is melting in water. The late Prof. TARR (1908, p. 97), in his account of the deposits formed on the stagnant waning ice sheets of Alaska, states that eskers are commonly found where the ice ended in bodies of standing water. He adopted the term "kames" (*ibid.*, p. 98) as distinct from eskers, and described kames as forming along the margins of the glaciers, and as attaining their best development where the gravel is deposited in lakes or on sheets of buried ice, which melts unaccompanied by deposition.

The marginal Irish eskers, according to this interpretation, agree with the great marginal bank of drift in Finland, which marks one stage in the retreat of the Finnish ice sheet. This bank, known as the "Salpausselka" (see, *e.g.*, SEDERHOLM, 1899, p. 15), it is worthy of remark, was built up where the ice sheet ended on the margin of the Yoldia Sea. Mr. W. B. WRIGHT (1914, pp. 39, 41) has already adopted the view that the Irish eskers "are more or less marginal deposits, perhaps entirely marginal," and that "the essential condition for the formation of eskers is the presence of stagnant water in front of the ice sheet during its retreat." Mr. WRIGHT regards this water as a series of local sheets of "ponded water"; he was not disposed to regard it as the sea.

### 5. *The Eskers a Littoral Formation.*

The members of the Irish Geological Survey who originally surveyed the eskers, especially KINAHAN, adopted the view that they were marine; and some were called "shoal eskers," on the grounds that they were formed as shoals by strong currents in a shallow glacial sea. The marine formation of the esker has been generally dismissed, but it seems nearer the truth than the later theories, which ascribed them to glacial rivers. The marine theory agrees best with their distribution. If the eskers had been formed by rivers in glacial canyons or in local bodies of "ponded water," there seems no reason for their practical restriction to the zone between the contours of 150 feet and 350 feet, and why they should not, as in

Sweden, continue to the highlands (*e.g.*, GEIKIE, 1894, p. 482).* Patches of esker-like drift occur at higher levels; they have been recorded at 464 feet in Iar-Connaught, and up to 542 feet about eight miles south-west of Roscommon; but the eskers of the typical esker district are all found below the level of 400 feet and mostly below the level of 350 feet (Map, fig. 11). They are, says HULL (1891, p. 127), "confined to the plains." KINAHAN placed the submergence beneath the "Esker Sea" as reaching the 300-foot contour (1878, pp. 225, 259, etc.) and SOLLAS (1896, p. 818) says the ground on which the eskers stand seldom rises more than 350 feet above sea-level.

The eskers range from Dublin to Galway and from Ballyhaunis as far south as Portumna, but in that wide area they do not occur above the level of 400 feet. In Tyrone, on the other hand, the eskers between Cookstown and Omagh are at the levels of from a little under 500 feet to over 700 feet (see *ante*, pp. 133–134). But the Tyrone eskers are different in character from those of the central plain; they are very irregular in level; for example, the esker which crosses the Cookstown Omagh road, near Barony Bridge, rises rapidly up the hill side and has the aspect of a terminal moraine, formed by a glacier that came down from the Pomeroy Hills. Its material, however, is sandy and its included stones are all washed and water worn; it is a glacieluvial marginal deposit.

In the typical esker district, on the other hand, the eskers disappear or occur as irregular mounds as they approach the contour of 350 feet. Thus the eskers of the Clara and Tullamore district are separated by a gap seven miles wide from their supposed continuation in the Philipstown–Edenderry Eskers. Their absence from the high ground west of Philipstown was probably due to non-deposition, as the land is above the esker level.

The Streamstown Esker is also significant as to the restriction of eskers by the 350-foot contour. From the heights marked on the maps and a view of the country from the railway I had regarded it as an exception to the rule; but a visit showed that it lies on the floor of a valley and that the higher ground on either side is free from eskers and esker-drift. This esker may have been formed of drifts deposited in a narrow gulf or in a strait connecting the arm of the sea that extended up the Inny Valley with that from Moate to Lough Ennell.

The relation of the eskers to the 300-foot contour is illustrated in fig. 11, which shows that across the middle zone of Ireland the eskers mostly occur below the 300-foot level, though they rise somewhat above it near Ballyhaunis. The main features in the distribution of the eskers in the area illustrated by that figure are:—

(1) Their restriction, with a few exceptions, to below the level of 300 feet.

(2) That when "esker drift" occurs above that level it is in scattered mounds, the "shoal-eskers" of Kinahan; as they are not ridges they are not eskers in the restricted sense of the term.

* The restriction also of the small river-formed eskers, as at Kilbeggan, to the low ground, is due to their formation where the river mouth emerged from the ice sheet to the plain or the sea.

(3) That the eskers have a more restricted distribution than the boulder clay, which is widespread and occurs at higher levels.

(4) That the eskers belong to four main groups :

(*a*) Those of the basin of the Clare River, east of Loughs Mask and Corrib, with occasional small eskers on the western edge of that basin ; its chief members are those of the Ballyhaunis–Dunmore district.

(*b*) The eskers of the Athenry district and of the streams discharging to the eastern end of Galway Bay.

(*c*) The eskers of the Shannon basin and its tributaries, the Inny, Brosna, Suck, and Kilcrow. This group includes the eskers of Ballinasloe, Athlone, Clonmacnois, Clara, Tullamore, Streamstown, Parsonstown, etc.

(*d*) The Roscrea, Clonaslee, Mountmellick and Maryboro Eskers, which lie around the northern foot of the Slieve Bloom Mountains and of other adjacent high ground.

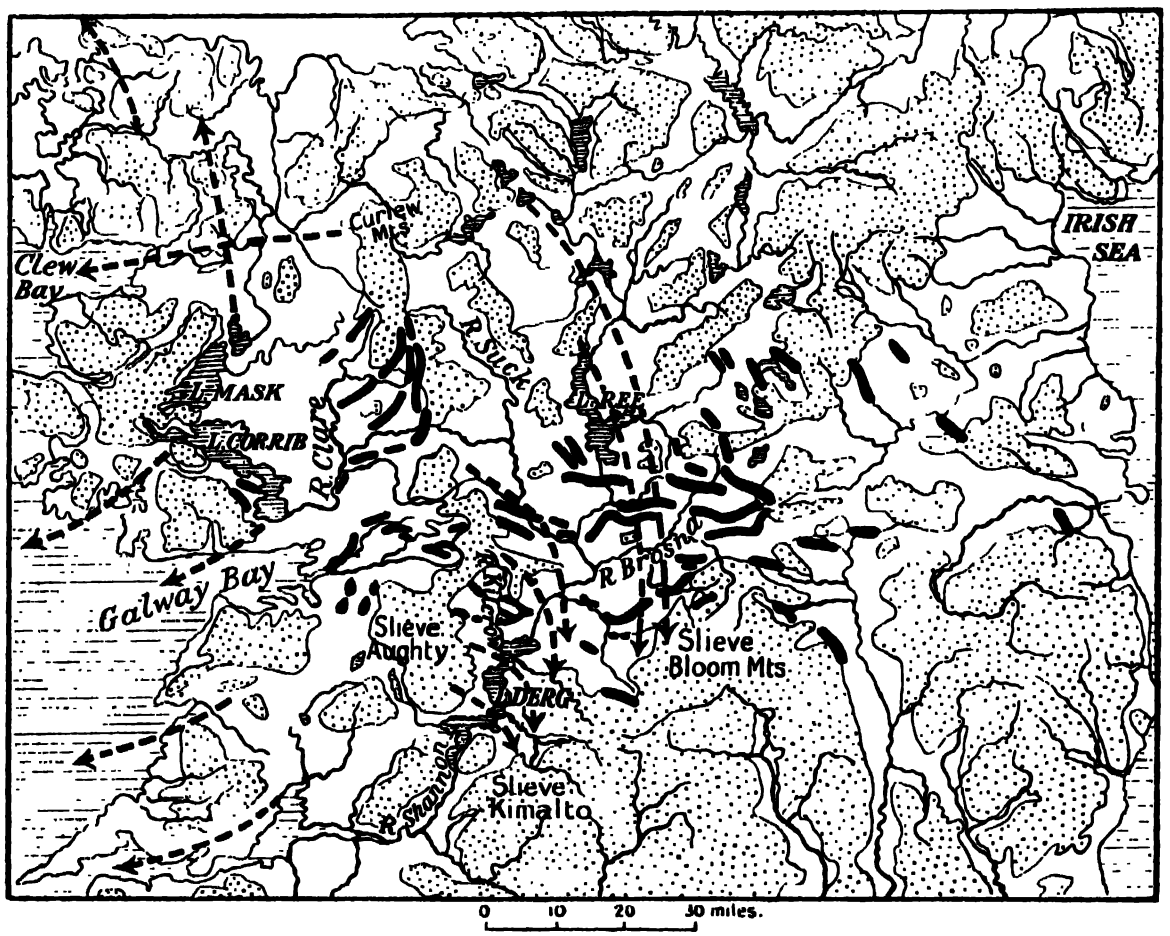



FIG. 11.—Sketch Map of the Irish Eskers in relation to the 300-foot contour; the areas above that contour are dotted ; the eskers generally end at that level. The chief exception is the north western group, which rise above 300 feet between the Clare and Suck Rivers. The broken arrows represent the course of the ice movement, after W. B. Wright ; they show that the chief eskers lie transverse to the ice movement.

Arrows indicating the ice flow are added from the map by Mr. WRIGHT (1914, p. 49), and they show that the chief eskers lie transversely to the movement of the ice. His map gives no definite directions for the Ballyhaunis district; but from the centre of ice accumulation to the east of Clew Bay and to the north-east of Lough Mask the ice flowed northward to the northern coast of Connaught, westward to Clew Bay, south-westward over Lough Corrib and western Galway. The position of the Ballyhaunis–Dunmore Eskers indicates their formation on the receding south-eastern edge of the Mayo ice sheet. Its recession left the Lough Corrib basin clear, and ice from southern Connemara was able to flow eastward past Galway to Athenry and Ballinasloe, carrying with it the boulders of granite from Iar-Connaught, which afford clear evidence of this movement. Some of this ice probably crossed the divide between Galway Bay and the Shannon, and reached Lough Derg through the valley of the Kilcrow River. This ice lobe then formed the eskers of the Killimor district, and later during its retreat those of the Athenry district.

Ice from the Curlew Mountains and other highlands of southern Sligo and Roscommon flowed south into the valleys of Suck and the Shannon, and reached the lowlands bounded to the south by Slieve Aughty, Slieve Kimalta and Slieve Bloom Mountains. Mr. WRIGHT'S arrows show that this Shannon glacier flowed transversely to the direction of the main eskers of Central Ireland; those of the eastern members of this series, such as the Long Hill near Ballygore, the Streamstown Esker, and those of the Inny were parallel to the main direction of this glacier, but they doubtless were the marginal formations along its eastern edge.

One remarkable contrast between the eskers of the Clare River and of the Shannon is that those of the Shannon basin are further to the south, which suggests that the Shannon glacier lasted longer than that which flowed into the Clare basin from Mayo, so that the emergence of the country prevented the formation of eskers during the recession of the ice from Lough Ree northwards. The dilapidated fragmentary condition of the western ends of the Ballyhaunis and Dunmore Eskers is consistent with their formation somewhat earlier than those in the Shannon basin.

The Roscrea, Clonaslee,* Mountmellick, and Maryboro Eskers were probably formed by ice which flowed down the northern slopes of the Slieve Bloom Mountains.

This sharp vertical limitation of the eskers is in favour of their formation having been controlled by a sheet of water, and this must have been either the sea or a glacial lake.

The difficulty in the assumption of a glacial lake is to account for the containing barriers. There is no difficulty regarding its northern and north-western margin, for that would be formed by the ice sheet itself. Partial boundaries would have been provided to the south-west by the Slieve Aughty Mountains, to the south by the Silvermines Mountains, and to the south-east by the Slieve Bloom Mountains; but these hills would leave wide gaps below the level of 350 feet, and even below 250 feet

* The Clonaslee Esker ranges up to 390 feet.

at Loughrea, Scarriff (140 feet), and the Nenagh-Curraheen gap (247 feet), while to the east of Tullamore there were wide tracts below the level of 350 feet. Unless all these outlets had been blocked by ice, there could have been no glacial lakes adequate for the formation of the eskers.

The extension of the sea across the esker plain presents no such difficulties. Some submergence of the British area during glacial times is now generally accepted; and even if this submergence were inadequate for the deposition *in situ* of the shells at 1300 feet on Three Rock Mountains south of Dublin, it was sufficient for the sea to have covered the Irish plain. Even the late CARVELL LEWIS, a most resolute opponent of the view that the British Isles were submerged in glacial times to the contour of about 1300 feet, accepted a submergence of 400 feet to the west of Dublin; and that amount would give the sea the range in Ireland required to explain the deposition of the eskers in a glacial sea.

The Irish eskers do not appear to be ordinary beach deposits, though KINAHAN at one time ('Mem. Geol. Surv., Ireland,' Explanation Sheet 128, 1859, pp. 29–30) compared them to raised storm beaches, in which the material is piled up with an arched dip down both slopes. The rejection of this hypothesis is not dependent on the absence or rarity of marine shells; for though OLDHAM'S paper (1844) shows that marine shell fragments are widely distributed in Ireland, they are certainly rare in the eskers. The absence of shells from these gravels does not, however, disprove their marine origin; for, as was pointed out by BROWN (1870, pp. 638, 688), many parts of the Greenland fiords, owing to the disturbed and muddy condition of the water, are "bare of marine life" and "unfavourable for sea-animals"; hence the deposits in them would be unfossiliferous. From the character of the esker materials any shells that might have been present would have been destroyed during its formation or dissolved subsequently.

### 6. *The Rarity of Fossils.*

The poverty of the marine fauna in both the Boulder Clay and the eskers is not surprising on the assumption that they were deposited in an ice-covered sea. NANSEN (1902, pp. 422–3) has pointed out that where the Arctic Sea is ice covered, owing to the absorption of light very few plants live in it. "We found," he says, "extremely little plant-life in the interior of the North Polar Sea, and it is as a rule in vain that Mr. H. H. GRAN has searched our plankton samples for diatoms." The poverty in plant-life involves the rarity of animal life. NANSEN refers to the extreme poverty of the plankton life in the Arctic Ocean (*ibid.*, p. 423; also vol. 4, 1904, p. 221), and to the unusually small amount of matter originating from organisms in the oceanic deposits. He says that it was "in most cases extremely difficult to find traces of shells of Foraminifera or other organisms," and that "I hardly found any Foraminifera in the Plankton samples taken in the North Polar Basin." He therefore attributes the few Foraminifera that were found to deposition when "the biological conditions

of the North Polar Basin were more favourable than they are now" (*ibid.*, vol. 4, p. 221).

As remarked by SCOULER (quoted OLDHAM, 1844, p. 64), the eskers were deposited "in shallow but turbulent waters, little favourable for the abode of molluscous animals." Even on open beaches in the Antarctic shells appear to be exceptional. According to Mr. JAMES MURRAY, the biologist with Sir ERNEST SHACKLETON'S first expedition, the action of the shore ice prevents the accumulation of shell beaches in the Antarctic. He states (1910, p. 2) that "on the shore there is no vestige of marine life, animal or vegetable, such as is found in the littoral zone of other coasts." "The presence of an ice-foot throughout the greater part of the year, and the grinding of ice along the coast where there is open sea, must destroy any living things which attempt to establish themselves. The zone thus kept devoid of life is of no great depth." HEDLEY (1916, p. 85) has remarked that the shell-bearing "raised beaches" of Macmurdo Sound are not shore beaches, but are probably upheaved from a deeper horizon.

If the eskers were deposited when the sea extended over Central Ireland to the contour of between 300 and 350 feet, the esker area would have been covered by a shallow bay, connected to the outer sea by narrow straits to the south-west and south, and with broader but still shallow channels to the east and south-east. This bay would have been occupied by ice-cold muddy water, swept by strong tides, and constantly churned up by waves from the calving ice front. The conditions would have been most unfavourable to animal life. Though the occurrence of shells would therefore be exceptional, they have been recorded in the eskers of Naas (380 feet) to the east, at Maryboro to the south-east, at Roscrea (400 feet) to the south, and at Moate (approximately 250 feet) in the centre of the esker area.

Madame LEMOINE'S determination of the nullipore from Ballinasloe is therefore consistent with the records of marine shells in the eskers of that part of Ireland.

### 7. *Definition of the Term Esker in Glacial Geology.*

When MAXWELL CLOSE (1867, pp. 211–212; see also KINAHAN and CLOSE, 1872, p. 6) separated drumlins from eskers, he accepted the latter term for fluvio-glacial ridges and mounds. In 1912 (No. 2), I summarised the history of the term kame and esker, quoted a series of authorities as to their usage, and followed Prof. T. C. CHAMBERLIN (1883, p. 300; renewed in 1899) in adopting the term kame for marginal fluvioglacial formations and osar or eskers for fluvioglacial ridges which are due to glacial streams, and occur on lines parallel to the flow of the ice. That definition, which has been often adopted in America, and Prof. SOLLAS'S interpretation of the Irish eskers, would restrict the term esker to fluvioglacial ridges deposited along glacial rivers. It would be synonymous with osar. The Irish eskers, however, include several varieties of fluvioglacial and glacieluvial ridges, and also mounds, and, if restricted to osar, the term would be limited to the least

extensive and important variety of eskers. G. H. Stone has proposed (1899, pp. 359–360) to "employ the term esker as a general term applicable to any mass or ridge of gravel irrespective of genetic classification," and that proposal is consistent with the Irish use of the term. The term osar was adopted by Jas. Geikie (1894, p. 169 ; spelt åsar) in preference to esker, and Stone accepted it in the same restricted sense. It seems best to follow their example and use the term esker in its original meaning for Irish ridges and mounds composed of glacial sand and gravel, and adopt osar, as the approximately phonetic rendering of åsar, for fluvioglacial ridges formed along glacial rivers. The term kame is then applicable, in accordance with general usage, for the marginal formations. According to this terminology, however, the major Irish eskers are kames.

The following classification summarises the structure of these drift formations as thus defined :—

(I) Drumlins—mounds composed of boulder clay.

(II) Osar—fluvioglacial ridges formed of sand and gravel deposited along the course of a glacial river and typically showing a transverse seasonal banding. Irish examples are those at Kilbeggan, near Clara, and the north-west of Athlone.

(III) Kames—ridges or mounds of sand or gravel deposited by water on the margin of a melting ice sheet. They consist either of fluvioglacial material where deposited by well defined streams and rivers ; or of glacieluvial material where deposited by the wash of water down the margin of an ice sheet or by water welling up along the margin of an ice sheet.

## V. Summary of Conclusions.

The Irish eskers belong to four groups.

I. The typical eskers on the Central Plain are kames, or marginal formations, deposited on the receding edge of an ice sheet. They are not moraines, as their materials were laid down by water and not dumped directly from melting ice. They were not formed along river beds, as adjacent segments vary greatly and irregularly in composition, patches of false-bedded sands and gravels alternating with coarse washed morainic drift ; the false-bedding and the variations in the composition of the eskers indicate that the material came from the side of the esker and was not carried along it. The predominant material in some eskers is a bouldery drift, which has been so washed that the ice-scratches have been destroyed ; in such places the material is glacieluvial.

That the main eskers were marginal is also indicated by their relation to the drumlins, of which the longer axis is regarded as lying in the direction of the ice flow. The main eskers are transverse to the drumlins.

The main eskers are also transverse to the ice movement as indicated by the striated rock surfaces and the distribution of the erratics where the rocks give evidence as to the direction of the ice movement. The main eskers lie between the levels of 100 feet

and 350 feet; they occasionally reach 400 feet. Their abrupt upward limit indicates that their range was controlled by some agent which was widespread over the plain of west central Ireland, but had a limited vertical range. These conditions are best provided by a sheet of water; and the melting of the ice as it entered a wide sheet of water best explains the heaping up of its material into a ridge instead of its deposition as a widespread sheet.

That this sheet of water was the sea is most probable for the following reasons:—

1. The underlying boulder clay and associated drifts contain foraminifera and marine shell fragments; these range up to 1,300 feet on Three Rock Mountain and appear to be widespread at lower levels.

2. Encrustations formed on boulders at Ballinasloe are identified by Madame LEMOINE as Lithothamnium.

3. The poverty of organisms is explicable by the present distribution of life under analogous conditions in the Arctic and Antarctic seas.

4. It is now generally agreed that large parts of the British area were submerged in glacial times to a sufficient height to have flooded the typical esker district of Central Ireland.

5. The alternative that the water was a glacial lake is improbable, as the esker sea was probably in existence after the ice had receded from the southern part of the central plain; and there would be no available southern margin for the lake.

II. A second type of esker consists of banded eskers lying within and transverse to the main marginal eskers, parallel to the direction of movement of the ice. They were probably deposited as delta deposits at the mouths of glacial rivers, and are thus equivalent to the Swedish osar.

III. In Tyrone, on the hills to the north and north-west of Pomeroy, is a third group of eskers, formed as glacieluvial marginal deposits around glaciers flowing from the hills.

IV. A fourth type consists of irregularly distributed mounds of fluvioglacial drift, as west of Athlone, which are probably due to the denudation of sheets of glacial sand and gravel.

The restriction of the term esker to any one of these four groups would be inconsistent with its original meaning. The term has been often defined so as to include only eskers of the second group, which in Ireland are relatively unimportant. The most typical eskers are those of the first group; they are kames, according to the widely adopted definition which uses the term kame for marginal formations. To avoid the use of the term esker with different meanings in geology and geography, its use is recommended as a general term for Irish ridges and mounds of glacial gravels and sands, and that of osar for fluvioglacial ridges which have been formed along the courses of glacial rivers.

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# V.—*The Thermo-elastic Properties of Muscle.*

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(From the Physiological Laboratory, Cambridge.)

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## (1) Introduction.

The thermal effects of applying a stress to a body were first studied by Weber (1), who found that when an iron wire was stretched a thermal effect was produced, and that the thermal change was proportional to the stress. Lord Kelvin (2) deduced the general equations of thermo-elasticity from the laws of thermodynamics, and proved that with stresses of the most general type the thermal effect is proportional to the applied stress, provided the material remains perfectly elastic. In a body which expands on being warmed, the effect of an extension is a *fall* of temperature, while a body which shortens on being warmed will show a *rise* of temperature on extension. It will be remembered that Engelmann found that some substances (*e.g.*, catgut) containing doubly refractive particles contract on heating; such bodies, therefore, would be expected to show a rise of temperature on being loaded, and the experiments given below prove that muscles and rubber belong to this class.

The phenomena of thermo-elasticity have been employed to demonstrate the stresses set up in structures on loading them; all that is necessary is to place the "warm" junctions of a suitable thermopile against the part it is desired to investigate, and then, on loading the structure in any desired manner, the magnitude and sign of the stress in that part can be determined at once from the deflection of a galvanometer. This method, which is quite reasonably simple to employ, appears to deserve a wider application than it has received. It could be applied to a variety of substances under a variety of conditions, *e.g.*, to the materials employed in the construction of aircraft, ships, guns, etc., in which considerable stresses have to be borne by structures which have to be kept as light as possible. It might even be employed in physiology to determine the distribution of stresses in the skeleton, and

it would certainly be of interest to make an extensive investigation of the thermo-elastic properties of elastic colloidal materials.

A further application is that of determining the elastic limit of a material. When an ordinary steel wire is stretched there is a fall of temperature; as the load is increased the fall of temperature increases at a proportional rate; at the elastic limit, however, the cooling is replaced by a warming due to the work done by the load being transformed irreversibly into heat instead of into elastic potential energy. The load at which this change occurs corresponds to the elastic limit of the wire.

Various applications of the method to engineering problems have been described by Coker (5 and 6).

It would seem that the employment of the light and sensitive thermopiles now obtainable, together with photographic recording as used in our experiments, might considerably increase the variety and importance of such applications. It should be remembered that metals and many other materials can bear enormously greater stresses, and so give greater thermal effects than can muscles or rubber, so that the high sensitivity of the galvanometer required in the experiments described here could be exchanged for a more rapid response, enabling a very accurate time-record of the thermal effects to be made. A more rapid response also could be secured by employing thinner insulation on the thermopile.

Our attention was first called to the subject by Mr. C. C. Mason, of the Cambridge and Paul Instrument Company, and it seemed desirable to investigate the phenomena of thermo-elasticity in living tissues. Assuming that (like catgut) a muscle shortens on warming, one would expect that on loading it there would be an evolution and on unloading an absorption of heat. These phenomena we have observed, but the results of our experiments are much more complex than those found in the case of an ordinary elastic body such as a steel wire, owing to the peculiar elastic properties of the muscle. The experiments throw considerable light on these elastic properties—which belong not only to muscles, but to many kinds of material—and, moreover, the purely physical thermal phenomena described here, if unheeded, may considerably interfere with or distort the physiological thermal changes associated with muscular activity.

Exactly similar results have been obtained in live and in dead muscles, and analogous results in the case of a rubber band, and it appears certain that the phenomena described are purely a consequence of the elastic properties of the material, and in no way dependent on the life or structure of the muscle.

The elastic property of a muscle which differentiates it from a steel wire is that, for any load, although well within the elastic limit, the muscle does not immediately attain its new length when the load upon it is changed. For example, when a weight is hung on a muscle, the muscle continues stretching for some time; when the load is removed, it returns only slowly to its original length. The same property is true of a jelly, or of a piece of rubber, and, of course, is well known to all who

have studied the properties of materials. The implications of it, however, are peculiar, and lead to complex and interesting thermal effects of applying a stress to the body concerned. The elastic property described is presumably due, in the case of a muscle, to the existence of an elastic network, colloidal or otherwise, containing a viscous fluid in its interstices. The final equilibrium value of the extension caused by a given load is presumably a characteristic of the network. When, however, the load is suddenly altered, the viscous fluid has to change its position within the network. and, if the alteration of load is rapid, the new equilibrium length is not attained until the viscous fluid has had time to reach its new position. Consequently, if the material be unloaded and allowed to shorten rapidly, doing work, the work done will be less than the work put into it in stretching it, and the difference between the two will cause an irreversible production of heat, complicating the reversible changes predicted by the thermodynamical reasoning.

The thermal effects of passive lengthening or shortening are by no means small. They are not as large as those of stimulating a live muscle, but they are large enough to afford a notable complication in the case of any contraction in which the muscle is allowed to shorten. A discussion of these complications is given below: one obvious means of avoiding them, and the one which—fortunately, though for other reasons—has been adopted by us in most previous work, is that of making the contraction isometric. In any experiments, however, in which a muscle is initially stretched, and allowed to shorten on excitation, the purely *physical* thermal effects consequent on the shortening and the subsequent extension during relaxation, must necessarily be superimposed upon the *physiological* thermal effects attending the chemical reactions set up by the stimulus.

### (2) Methods and Results of Thermal Experiments.

The instruments employed have been those described elsewhere (3). The use of the combined muscle-chamber and thermopile, immersed in well stirred water in a large double-walled vacuum flask, has ensured an absence of differences of temperature at different points on the muscle which were the stumbling block in all previous experiments in which the muscles were allowed to move over the junctions (4). The uniform temperature of the whole thermopile and muscle eliminated the possibility of a movement bringing cooler or warmer parts of the muscle on to the junctions. The muscles (a pair of sartorii from *Rana temporaria*) were fitted on the thermopile in the chamber, and a long thread taken from their upper ends, through the tube holding the chamber, up to one arm of a pivoted lever; to the other arm of the lever was tied a thread carrying a pan, in which were placed the weights required to load the muscle. The lever itself had a small weight, usually of the order of 5 grm., fixed directly to it, to provide a small constant tension on the muscle. The loading or unloading of the muscle was carried out by hand, by gently raising or lowering the pan in which the weights

were placed. For example, if it were desired to investigate the effects of loading the muscles with 60 grm., the weights were placed in the pan and the pan held in the hand with the thread attaching it to the lever loose; the muscle was then subject only to the load of the 5 grm. providing the small constant tension. When all was ready, and the photographic arrangements running, on a given signal, recorded on the photographic paper, the pan, with its weights, was gently lowered so as to hang on the lever, and subject the muscle to an additional tension of 60 grm. The deflection of the galvanometer was recorded on the paper and the record allowed to run as long as required, usually for about 30 seconds. To investigate the effects of *unloading*, the load was allowed to hang on the lever for some time, say 2 or 3 minutes, until the length of the muscle had become appreciably constant; on a given signal, the pan with its weights was gently lifted, and the photographic record made as before. Typical records are shown in fig. 1. It should be noted that the load was lowered *gently* on to the muscle and gently removed, particular care being taken to avoid anything in the nature of a jerk.

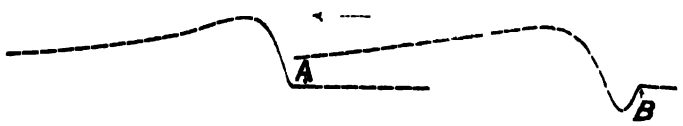



FIG. 1.—Pair of sartorius muscles from *Rana temporaria*. Permanent load 5 grm. At A on the left hand curve 155 grm. was hung gently on the muscle: the temperature rose. At B on the right hand curve, after the 155 grm. had been hanging on the muscle for some time, it was gently removed: the temperature fell rapidly (the reversible effect) and then rose (the irreversible "viscous" effect) and finally fell again (the physical loss of heat by conduction). Time in secs. shown on the curves. N.B. These and all other records given here read from right to left.

In order to obtain satisfactory records, it was usually desirable to increase the sensitivity of the galvanometer to about $1\frac{1}{2}$ times that employed in the case of experiments on the heat-production of stimulated muscles.

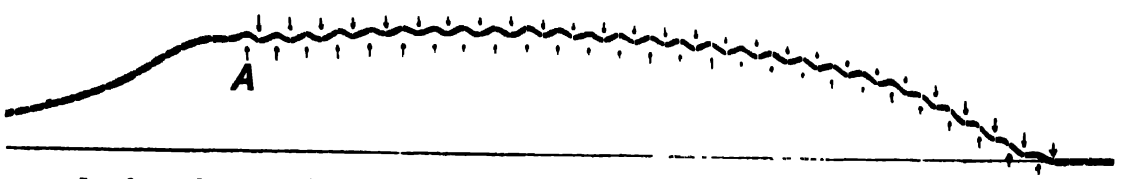



FIG. 2.—Dead muscles at 11° C. 163 grm. load "on" and "off" at intervals of 1 sec. (*i.e.*, load on—1 sec. interval—load off—1 sec. interval—load on—etc.). 50 ohms in galvanometer-thermopile circuit to reduce sensitivity, which in this experiment was about 0·26 of that in the experiment shown in fig. 1. Notice (*a*) the rise of temperature on loading followed by (*b*) the fall of temperature on unloading; superimposed upon (*c*), the gradual steady rise of temperature to a maximum (determined by a balance between heat produced and heat lost). Of these (*a*) and (*b*) are the reversible thermodynamic effects; (*c*) is the irreversible effect due to the viscous flow accompanying extension and shortening. The arrows above the curve indicate the moments at which loading occurred: the arrows below the curve indicate the moments at which unloading occurred. Time marks in secs. on the curve. At A the muscle was unloaded finally, and after a short delay began to cool down by simple loss of heat.

Various other procedures were adopted to illustrate the phenomena. For example, in some experiments the pan containing the weights was raised and lowered gently at regular intervals of, say, one second. Fig. 2 is a record of the thermal effect of such a procedure. In other experiments the muscle was loaded and then unloaded after a certain definite interval, the effect of which is shown in fig. 3.

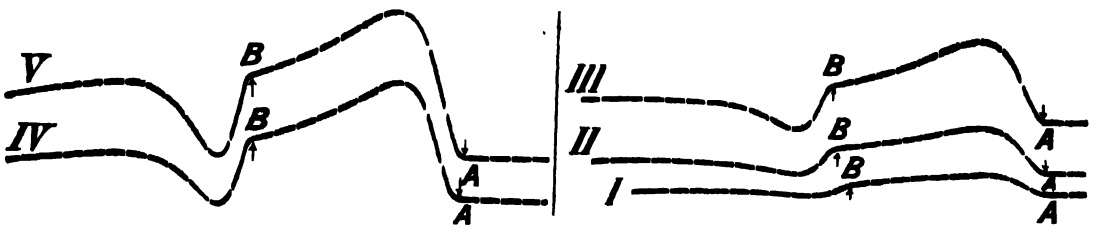



FIG. 3.—Dead muscles at −0·6° C. Various loads "on" and "off" at an interval of 10 secs. At A on each curve the load was put "on," at B it was taken "off." Curves I–V show respectively the thermal effect of loading and unloading with 20, 50, 95, 155, and 200 grm. Time marks in secs. on the curves. Notice (*a*) the sudden rise of temperature on loading, and (*b*) the sudden fall of temperature on unloading, followed by (*c*) a subsequent rise. The shape of the curves is determined largely by loss of heat through conduction. Note also that the thermal effect increases as the load is increased, but not quite proportionally.

Exactly similar results were obtained with live and with dead muscles, and there is no evidence to show that the phenomena are in any way connected with the life or mechanism of the muscle. To make the more certain of this, the observations were repeated with a narrow strip of an old Dunlop rubber tyre (inner tube), more or less of the shape and size of a pair of muscles, and lying upon the junctions of the thermopile in the same way. In order to make the motion of the rubber over the junctions more free, a drop of paraffin oil was placed upon the thermopile. The phenomena shown by the rubber were similar in type to those shown by the muscle, though quantitatively different. Fig. 4 shows the characteristic effects of loading and

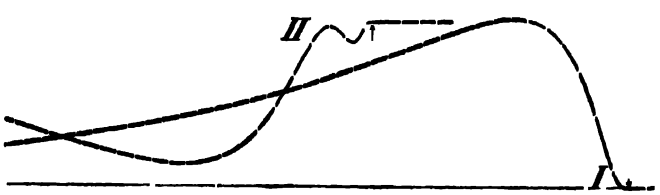



FIG. 4.—Strip of old rubber tyre, 3·5 cm. long, mass 0·59 grm., of the general shape of a pair of sartorius muscles, placed upon the thermopile in the muscle chamber at 11° C. Permanent load 150 grm. Time shown in secs. on the curves. Curve I shows the rise of temperature on loading the rubber with a further 550 grm. Curve II shows (*a*) the fall; (*b*) the rise; and (*c*) the subsequent further fall of temperature on removing the 550 grm. NOTE.—In curve I an extra 25 ohms was put in the galvanometer-thermopile circuit in order to reduce the sensitivity; consequently Curve I is on 2·4 times the scale of Curve II.

unloading the rubber. In this case there was a permanent load of 150 grm. on the rubber, and an extra load of 550 grm. was put on and taken off. Fig. 5 shows the

effects of loading followed by unloading at various intervals—1, 2, 4 secs. and "infinity."

The sensitivity, expressed in degrees Centigrade per millimetre deflection, was

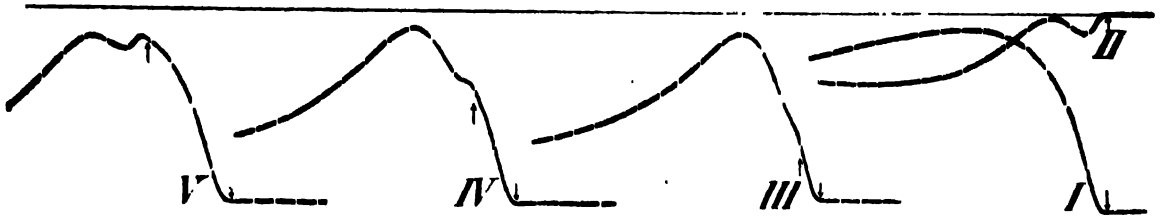



FIG. 5.—Strip of old rubber tyre, as in fig. 4. Permanent load 150 grm.

Curve I shows the rise of temperature on loading with a further 300 grm.

Curve II shows (*a*) the fall; (*b*) the rise; and (*c*) the subsequent further fall of temperature on removing the 300 grm., after it had hung on the muscle for an "infinite" time.

Curve III shows the effect of loading with 300 grm., and then unloading again after 1 sec.

Curve IV shows the effect of loading and unloading again after 2 secs.

Curve V shows the effect of loading and unloading again after 4 secs.

By an analysis of the curves of fig. 5, taking the deflections of I and II at every 1 sec. and then adding them together algebraically with an interval ("phase difference") of (*a*) 1 sec., (*b*) 2 secs., and (*c*) 4 secs., it is found that as regards the *initial* shape of the curve—*i.e.*, up to 5 or 6 secs.—there is good agreement between the results so calculated and the observed Curves III, IV, and V respectively. Afterwards, however, in all the later stages, much less heat is actually given out than would be calculated from the addition of I and II with the appropriate "phase difference": in fact—as would be expected—the irreversible processes leading to a loss of potential energy and the production of heat, are much less in extent when the load is left on for a shorter time. The same thing is shown by the fact that the total heat production in the complete cycle of loading and unloading, given very nearly by the areas of the Curves III, IV, and V, obviously increases as the interval between loading and unloading increases.

determined in the case of the experiments on muscles by means of a direct calibration, as described in another paper (3). It was about the same in the various experiments on muscles and may be taken to be approximately (in the original records)

$$1 \text{ mm.} = 6 \times 10^{-5}\ \text{C. or } 0{\cdot}00006 \text{ calories per grm.}$$

One is, of course, working to a high sensitivity in these thermal measurements, as the records are reliable to about 0·1 or 0·2 mm., which means that one is reading to about 10 millionths of a degree. A less sensitive arrangement would not show to sufficient accuracy the rather small quantities involved.

[The curves as reproduced in figs. 1 to 5 have been reduced to about 40 per cent. of their original size.]

In the case of the experiments on the rubber strip a direct calibration was not possible, as the rubber is a non-conductor of electricity, and so no warming current could be applied to it. We may, however, assume for the purposes of a rough calculation of the coefficient of thermal expansion that the sensitivity in degrees Centigrade was the same as in the muscle experiments.

The sensitivity of the arrangement may be expressed also in the following form, by employing the mechanical equivalent of heat:—

1 mm. = 2·5 grm.-cm. of work per gramme of muscle.

This means that, for a pair of muscles weighing 0·16 grm., 1 mm. deflection is given when 0·4 grm.-cm. of work is absorbed by the muscles and degraded into heat. A full deflection of 6 cm. could be produced, therefore, by the absorption of mechanical work to the extent of 24 grm.-cm. This is a more expressive way of stating the sensitivity, as it is clear that 24 grm.-cm. is of the same order of size as the work done in stretching the muscle 1 cm. with a load (say) of 100 grm., whereas 0·0036 calories has at first sight no obvious relation to the same quantity.

In most of the experiments the thread connecting the muscle to the lever was free in the tube; in a few of them, however, the narrow part of the tube (about $\frac{3}{4}$ mm. diameter) was filled with vaseline and the thread moved in the vaseline. The vaseline had the effect of reducing the irreversible rise of temperature following the reversible fall of temperature caused by unloading the muscle. This fact is of interest in confirming the theory as given here, and will be discussed below.

### (3) Discussion of Thermal Experiments.

Since the phenomena described are susceptible to some degree of an exact treatment by the methods of thermodynamics, it may be well to put on record here a deduction of the equations for a finite extension of an elastic string. We have thought it better to employ the conception of "free energy," rather than that of "entropy," as being more intelligible to the average reader. The principle involved is to calculate A, the free energy, *i.e.*, the maximum work which could be done by an extended string, and then, by the second law of thermodynamics, to equate $dA/dT$ to Q/T, where T is the absolute temperature and Q is the heat absorbed in the process. If the coefficient of thermal expansion be known, $dA/dT$ can be calculated, and therefore Q is obtained directly from the equation

$$Q = T\frac{dA}{dT}. \tag{1}$$

Let an elastic body shorten from length $l_1$ to length $l_2$, doing work, and suppose the length is $l$ for a tension P. Then the free energy of the change is

$$A = \int_{l_2}^{l_1} P dl.$$

Differentiating with respect to T

$$\frac{dA}{dT} = \int_{l_2}^{l_1}\left(\frac{\partial P}{\partial T}\right)_l dl, \tag{2}$$

where $\left(\frac{\partial P}{\partial T}\right)_l$ is the rate of change of P with respect to T when $l$ remains constant.

Now $l$ is a function of two variables, and of two variables only, P and T: hence we may write, when $l$ remains constant,

$$\delta l = 0 = \left(\frac{\partial l}{\partial P}\right)_T \delta P + \left(\frac{\partial l}{\partial T}\right)_P \delta T$$

from which

$$\left(\frac{\partial P}{\partial T}\right)_l = -\left(\frac{\partial l}{\partial T}\right)_P \Big/ \left(\frac{\partial l}{\partial P}\right)_T. \tag{3}$$

Now, if the coefficient of thermal expansion $\alpha$ be independent of the tension P, we have

$$\left(\frac{\partial l}{\partial T}\right)_P = \alpha l. \tag{4}$$

In this case, from (2), (3) and (4), we have

$$\frac{dA}{dT} = -\int_{l_2}^{l_1} \alpha l \left(\frac{\partial P}{\partial l}\right)_T dl.$$

Integrating by parts

$$\frac{dA}{dT} = -\alpha (P_1 l_1 - P_2 l_2) + \alpha \int_{l_2}^{l_1} P dl.$$

Hence from (1) above, the heat absorbed is given by

$$Q = \alpha T [\text{work done} - (P_1 l_1 - P_2 l_2)]. \tag{5}$$

This is the most general form of the result but, if we may assume that the body is perfectly elastic, we may write

$$\text{work done} = \tfrac{1}{2}(P_1 + P_2)(l_1 - l_2)$$

in which case

$$Q = -\tfrac{1}{2}\alpha T (P_1 - P_2)(l_1 + l_2). \tag{6}$$

In other words, when the tension is diminished heat is *evolved* equal to

$$\alpha T \,(\text{diminution of tension})\,(\text{mean length}),$$

and when the tension is increased, heat is *absorbed* equal to

$$\alpha T \,(\text{increase of tension})\,(\text{mean length}).$$

It should be noted that here we have measured everything, including the heat, in dynamical units; if the heat be measured in calories, the tensions in grams-weight and the lengths in centimetres, the heat absorbed becomes

$$\frac{\alpha T \,(\text{increase of tension})\,(\text{mean length})}{4{\cdot}24 \times 10^4} \text{ calories.}$$

If we consider the fall of temperature in an adiabatic extension instead of the heat absorbed in an isothermal one, the fall of temperature $(-\delta T)$ is given by

$$-\delta T = \frac{\alpha T \,(\text{increase of tension})\,(\text{mean length})}{(\text{mass})\,(\text{specific heat})\,4{\cdot}24 \times 10^4}. \tag{7}$$

In the case of most substances $\alpha$, the coefficient of thermal expansion, is positive and of the order $10^{-5}$. In the case of muscle and of rubber it appears to be negative, but of the same order of size. With these substances there is an initial rise of temperature on increasing, and an initial fall of temperature on decreasing, the tension.

We have assumed in the preceding argument that we have to deal with a perfectly elastic body undergoing a reversible change. In the case of a substance like muscle the change will be reversible only if carried out infinitely slowly, for otherwise an irreversible degradation of potential energy into heat under the action of viscous forces will occur. This matter also can be treated by means of thermodynamical reasoning. In fig. 6 are shown curves relating the extension of a muscle to its

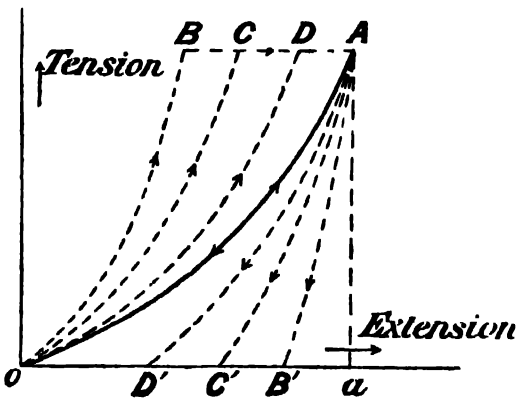



FIG. 6.—Relation between tension and extension in a muscle. The full curve OA corresponds to a very slow process of unloading or loading the muscle from or to a given tension, and represents a "reversible" process. The dotted curves represent "irreversible" processes carried out more or less rapidly. The curves OBA, OCA, and ODA correspond to *loading* carried out rapidly, the most rapid being OBA, and the least rapid ODA. The curves AB'O, AC'O, AD'O, correspond to unloading carried out rapidly, the first being the most and the last being the least rapid. The potential energy possessed by the stretched muscle corresponds to the area OA$a$: the work done in stretching it rapidly along (say) the curve OCA corresponds to the area OCA$a$: the work obtained from it on unloading it rapidly corresponds (say) to the area AC'$a$: the work lost and degenerated into heat irreversibly in the complete cycle corresponds therefore to the area OCAC'.

[NOTE.—The curves are illustrative only and do not represent an actual observation.]

tension. The curve OA represents the relation of extension to tension when the tension is increased exceedingly slowly from the value zero to the value A$a$, and the work done in extending the muscle is represented by the area OA$a$. The process of passing from O to A or from A to O is strictly reversible, and no work or potential energy is degraded into heat in the process. If, however, the tension be increased more or less rapidly from zero to the value A$a$, the relation between extension and tension follows one or other of the curves OBA, OCA, or ODA: OBA representing the more rapid change and ODA the less rapid. In the case of the rapid change corresponding (say) to OCA, the work done in stretching the muscle corresponds to the area OCA$a$, which is greater by the area OCA than the *greatest* amount of work which can be recovered on allowing the muscle to shorten again. Hence in this rapid stretching the work done re-appears in the muscle, partly as mechanical potential energy corresponding to the area OA$a$, and partly as heat corresponding to the area OCA. The more rapidly this stretching process is carried out the greater will be the

amount of work re-appearing irreversibly as heat in the muscle. The irreversible transformation of work into heat is presumably caused by the rapid flow of viscous fluid inside the network, colloidal or microscopic, of the muscle. Hence, on stretching the muscle rapidly by increasing the tension on it, there will be a production of heat under two headings—

($a$) The reversible thermodynamic effect given by the formula deduced above,

$$Q = \tfrac{1}{2}(-\alpha)T(P_1-P_2)(l_1+l_2);$$

($b$) The irreversible effect corresponding to the area OCA in the diagram.

These effects are of the same sign and additive.

When the muscle is unloaded a similar process takes place. If unloaded infinitely slowly, the extension-tension relation follows the curve AO. If unloaded more or less rapidly, it follows one or other of the curves AB′O, AC′O, AD′O. The *maximum* work obtainable from the stretched muscle is given by the area AO$a$. The work obtained in a rapid shortening corresponds to one or other of the areas AD′$a$, AC′$a$, AB′$a$, the area AB′$a$ corresponding to the more rapid process. Consequently, in shortening rapidly along (say) the curve AC′O work is lost corresponding to the area AC′O, the potential energy of the stretched muscle re-appearing partly as external work equal to the area AC′$a$ and partly as heat equal to the area AOC′. This irreversible transformation of potential energy into heat also is presumably due to the flow of viscous fluid inside the elastic network of the muscle. Thus, on unloading the muscle rapidly there will be two different thermal effects: –

($a$) The reversible thermodynamic effect given by the formula deduced above, viz., an absorption of heat equal to

$$\tfrac{1}{2}(-\alpha)T(P_1-P_2)(l_1+l_2);$$

($b$) The irreversible production of heat corresponding to the area AC′O in the diagram.

These effects are of opposite sign and lead to the complex curves of unloading shown in figs. 1 to 5.

A further interesting case arises in the alternation of loading and unloading at a finite interval, as shown in figs. 2, 3, and 5. Here the relation between tension and extension follows a set of curves more or less similar to those shown in fig. 7. When the muscle is loaded, the extension follows the curve OA; as it remains loaded it stretches at constant tension from A to B, from A to C, or from A to D, according as a shorter or a longer interval is given. If the muscle be unloaded a short time after it is loaded, the complete cycle is represented by the curve OABG; if the interval be longer, by the curve OACF; if still longer, by the curve OADE. Thus, if the interval between loading and unloading be short, work corresponding only to the area OABG is degraded into heat, while if the interval be greater more work is lost, corresponding to the area OADE. In any case, however, some work is lost. Thus,

in addition to the reversible thermodynamic effects corresponding to loading and unloading, there is an irreversible production of heat, corresponding in each cycle to

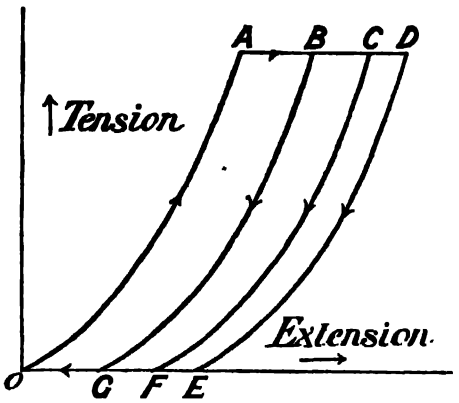



FIG. 7.—Curves relating tension and extension in the case of a complete cycle made up of a rapid process of loading and a rapid process of unloading separated by a finite interval. OA represents the loading curve; BG the unloading curve after a short interval; CF the unloading curve after a longer, and DE after the longest interval. The work degraded into heat irreversibly in the complete cycle, OACF, corresponds to the area OACF, and is clearly greater the greater be the interval between loading and unloading.

[NOTE.—These curves are illustrative only and do not represent an actual case.]

(say) the area OACF, and appearing in fig. 2 as the steady displacement of a curve on which are shown oscillations corresponding to the reversible alternations of heat production and absorption. The same phenomenon is shown in another way in fig. 5. Here the thermal effects of loading and unloading are shown in curves I and II, III, IV, and V, with intervals between them of "infinity" and of 1, 2, and 4 seconds respectively. It can be shown, both experimentally and theoretically, that the total heat produced corresponds fairly accurately to the area of the photographic record, and it is obvious that the areas of curves III, IV, and V are in ascending order of magnitude, corresponding to the increasing interval between loading and unloading. This is a strong incidental verification of the theory sketched above.

A further verification of it is shown by the following observation. In most of the experiments the thread connecting the muscles to the load passed up freely through a narrow dry tube, but in those few in which the tube was filled with vaseline, and the thread passed through the vaseline, it was obvious that the secondary and irreversible rise of temperature following unloading was far smaller than in the other experiments. The reason is simple. It required a definite, if small, force to pull the thread through the vaseline at a finite rate, so that the unloading process really took place very much more slowly, the muscle being held to some extent by the vaseline, and giving up its potential energy gradually in warming the vaseline instead of warming itself. By allowing the muscle to shorten even more slowly, the method might be extended and the irreversible thermal effects eliminated almost completely.

By means of the method of analysis described in another paper (3) it is possible

to determine the rate of heat-production at all moments subject to loading or unloading and to exhibit it in a curve. The details of such an experiment are given below and the results are shown in fig. 8.

*Experiment.*—Pair of sartorius muscles. Permanent load, 7 grm. Extra load of 50, 100, 150, or 200 grm. put "on" or taken "off." Control curves made by electrical warming with 7, 57, 107, 157, and 207 grm. on; the initial shapes of the five sets of control curves agreed exactly. By means of the control curve the loading and unloading curves were analysed. The unloading curves are complex, owing to the mixture of production and absorption of heat; the analysis of them is difficult, and in such a case the results are necessarily rather indeterminate. The loading curves, however, are easy to analyse, and the following analysis of the thermal effects of loading with 200 grm. is typical. Heat production is given on an arbitrary scale in units per $\frac{1}{4}$ second :—

| Time, secs. | 0 | $\frac{1}{4}$. | $\frac{1}{2}$. | $\frac{3}{4}$. | 1. | $1\frac{1}{4}$. | $1\frac{1}{2}$. | $1\frac{3}{4}$. | 2. | $2\frac{1}{4}$. | $2\frac{1}{2}$. | $2\frac{3}{4}$. | 3. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Heat production | 56 | 14 | 8 | 4 | 3 | 2 | 2 | 2 | 2 | 3 | 2 | 2 | 1 |

After 3 seconds the heat production continued more or less uniformly at the rate of 1 unit per $\frac{1}{4}$ second for some time. The results are shown in fig. 8. The analysis of the unloading curve shows that there is an absorption of heat, following more or less the type of relation shown in fig. 8, but having superimposed upon it a production of heat starting later and falling more rapidly. The absorption of heat is initially the faster, then becomes the slower, and finally the faster again.

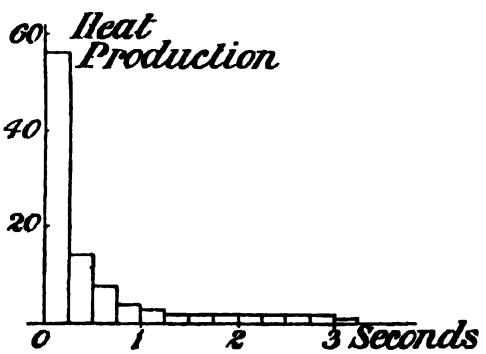



Fig. 8.—Pair of sartorius muscles, permanent load 7 grm., loaded with extra 200 grm. Record analysed and heat production shown in arbitrary units at every $\frac{1}{4}$ sec. following loading. For description of experiment see above.

## (4) Results and Discussion of Mechanical Experiments.

A further experimental confirmation of the theories described above may be gained by the use of the inertia system of obtaining the maximum work described by one of us recently (7). A muscle, alive or dead, is connected to the inertia lever by a long thread: the lever is then loaded with a small rider to record the work performed, and a large rider to stretch the muscle. The large rider hangs from a long thread, and, when all is ready, is suddenly lifted off the lever; the stretched muscle immediately proceeds to shorten, and gives out all the work of which it is capable in accelerating the lever: the work done is measured by the distance through

which the small rider is lifted. If the moment of inertia of the lever were infinite, the stretched muscle would shorten infinitely slowly, and give out all its elastic energy as work; the moment of inertia, however, being relatively small, the muscle shortens rapidly, and therefore gives out considerably less work. By loading the muscle with different weights and noting the extension produced, it is possible to construct a curve relating extension to load, such as the curve OA in fig. 6. From this, the potential energy corresponding to any given load can be read off as an area. This potential energy can then be compared with the actual work performed on the inertia lever in an ordinary rapid shortening consequent on release. It is found that the actual work done in a rapid shortening may be very considerably less than the potential energy of the muscle, *i.e.*, than the work which would be done in a very slow shortening; consequently, in a rapid shortening, a large part of the potential energy is wasted, and can only reappear as heat. The following Table gives typical results :—

TABLE I.—Comparison of the work done in the rapid shortening of a passively extended muscle, with the elastic potential energy possessed by the muscle in virtue of its stretched condition.

NOTE.—The action of the muscle pulling on the inertia lever is similar to that of the muscle pulling horizontally on, and so accelerating, a mass, M, suspended freely by a long string. The "equivalent mass," M, of the inertia system was varied in the following experiment, in order to vary the rate at which the muscle shortened; the greater the "equivalent mass," the more slowly will the muscle shorten. We should expect, therefore, to find more work done when the "equivalent mass" is greater, and this proves to be the case.

The potential energy is calculated from the area of the curve relating tension to extension; this and the work done are expressed in grm.-cm.

EXPERIMENT 1.—Pair of Sartorius Muscles of *Rana Temporaria*.

| Load on Muscles, grm. weight. | 5½. | 7. | 8½. | 11. | 17½. | 27. | 42. | 57. | 82. |
|---|---|---|---|---|---|---|---|---|---|
| Work done, M = 520 grm. . . . | 0·7 | 1·0 | 1·3 | 1·5 | 2·2 | 3·2 | 4·6 | 6·1 | 8·8 |
| Work done, M = 910 grm. . . . | 0·8 | 1·0 | 1·3 | 1·7 | 2·5 | 3·5 | 5·0 | — | — |
| Work done, M = 1300 grm. . . | 1·0 | 1·3 | 1·6 | 2·0 | 2·9 | 4·2 | 5·9 | 7·6 | 10·1 |
| Potential energy (M = ∞) . . . | 1·0 | 1·4 | 1·9 | 2·5 | 3·8 | 6·0 | 9·4 | 14·2 | 20·8 |

EXPERIMENT 2.—"Equivalent Mass," M = 2900 grm.

| Load on Muscles. | 8. | 10. | 13. | 17. | 26. | 40. | 63. | 86. | 123. |
|---|---|---|---|---|---|---|---|---|---|
| Work done . . . . | 1·3 | 1·8 | 2·3 | 2·9 | 4·1 | 5·5 | 8·4 | 10·9 | 14·7 |
| Potential energy . . . | 1·3 | 1·9 | 2·7 | 3·6 | 5·5 | 9·0 | 16·2 | 23·4 | 37·2 |

We see from these experiments that *the work done by a muscle in shortening rapidly when suddenly unloaded is less than the potential energy it contains*, and considerably less for large loads; moreover, Experiment 1 shows that, as the rapidity of shortening diminishes (with increasing "equivalent mass"), so the amount of work obtained increases. These facts confirm the theory discussed in connection with fig. 7 above, and have a considerable bearing on the mechanics of muscular contraction, as will be shown later.

There seems, therefore, to be little doubt that the theory employed to explain the thermal effects of loading and unloading, as shown in figs. 1–5, is correct.

## (5) Application to Physiological Problems.

The importance of the phenomena described here can be discussed best under two headings: (*a*) in relation to the heat-production of muscles, and (*b*) in relation to the mechanics of muscular contraction.

### (a) *Heat-production.*

Only if a muscle be held rigidly isometric will the heat produced in consequence of a stimulus be free from the complicating effects of the thermo elastic phenomena described above. If the muscle be allowed to shorten, even as little as 1 mm., the effect will be seen. In analysing the time-course of the evolution of heat in the earlier stages of a muscular contraction (3), we have noticed more than once that, in addition to the ordinary thermal effects, the analysis required a small evolution of heat, followed by an equal small absorption of heat, corresponding in time to contraction and relaxation respectively; and it was noticed in all such cases that the muscle had been able, by reason of being tied by a long and somewhat extensible thread, to shorten 1 mm. or 2 mm., instead of being, as in most experiments, held rigidly isometric by direct attachment to the upper end of the thermopile. It is clear, therefore, that, where possible, it is safer and simpler to employ rigidly isometric contractions in all investigations of the heat-production of muscles. It is advisable also, when employing a "tension lever," to record the tension set up in an isometric contraction, to ensure that only the minimal shortening is necessary in order to work the lever,* and that the connections to the lever are as inextensible as possible (*e.g.*, not made of silk thread, which stretches considerably). If such precautions be taken, it is possible to avoid largely, if not entirely, the errors and complications caused by the phenomena described here.

In many experiments, however, and in the very important experiments in which work is actually done by the muscle, it is not possible to employ isometric con-

* In order to avoid any appreciable shortening of the muscle it is advisable to adopt a photographic device giving high magnification of movement for recording the tension developed by a muscle. Such a device was used in making the curves shown in fig. 12, of the paper (3) describing the methods employed in this investigation.

tractions. In all such cases, the actual heat-production observed is the resultant of the thermal effects of mechanical shortening or extension, and of the physiological effects set up by the stimulus. This is still further complicated by the fact that, during relaxation, the part of the potential energy set free on excitation which has not been used up in doing work is irreversibly degraded into heat. The matter can, however, be made rather more intelligible by the consideration of a physical analogy. It will be seen from this that, if a muscle, whether excited or not, be released and allowed to shorten, we may expect to find an absorption of heat, in addition to the absorption of mechanical potential energy transformed into work. If the muscle be subjected to a high initial tension, we may expect the initial absorption of heat to be greater. If the tension in an unexcited muscle carrying a weight be provided by one part (A) of the muscle, while the "active" physiological increase of tension consequent on excitation is provided by another part (B), *e.g.*, if the initial tension be taken by inactive connective tissue fibres, while the development of tension is due to active muscle fibres, then the problem is simple, for it is clear that each part can be considered separately; in this case, it is obvious that, when the whole system shortens, doing work, the usual *physical* thermal consequences of shortening must take place in the part (A) of the system, in addition to the combined physical and physiological effects in the part (B). If, however, (A) and (B) be the same, *i.e.*, if the passive tension of the loaded but unexcited muscle be provided by the same fibres or network as develop the extra tension on excitation, the matter is not so simple, and we must consider the thermal consequences of shortening in the excited muscle as a whole. The correct way of regarding the question then is best made clear by considering the following physical analogy.

### *A Physical Analogy.*

Consider a soap-bubble of radius $r$, consisting of a film with surface-tension $\beta$. The surface energy of the bubble is then $4\pi\beta r^2$, and the maximum work obtainable, by allowing the bubble to contract from radius $r_1$ to radius $r_2$, is $4\pi\beta(r_1^2-r_2^2)$. Thus the bubble is analogous to an unexcited muscle subjected to an initial tension, and is capable similarly of doing work, if allowed, at the expense of its stored potential energy. There is, moreover, a further analogy with the muscle. Surface-tension, in general, diminishes with rise of temperature, and, from this, it can be shown thermodynamically that there is a reversible production of heat when the bubble contracts, and similar absorption of heat when the bubble expands; these thermal effects are analogous to those shown on loading or unloading a muscle.

The free energy, A, of the contraction of the bubble is given by

$$A = 4\pi\beta(r_1^2 - r_2^2).$$

Employing the thermo-dynamic equation

$$Q = T\frac{dA}{dT}$$

we find that the heat *absorbed* is given by

$$Q = 4\pi T(r_1^2 - r_2^2)\frac{d\beta}{dT}.$$

But $d\beta/dT$ is negative for actual films of fluid (8) and may be put constant and equal to $-k$, so that the heat *produced* is given by

$$Q = 4\pi kT(r_1^2 - r_2^2).$$

Consider now the case of a soap-bubble which, by some active process, following what (to make the analogy clearer) we will call "excitation," increases its surface tension from $\beta$ to $\beta'$. Many such processes might be considered, *e.g.* :—

(*a*) The oxidation of a surface film of some substance, such as oil, which previously lowered the surface tension of the water composing the bubble;

(*b*) The neutralisation of an electric charge on its surface (in this case the mathematical statement is slightly different from that given here);

(*c*) The liberation of some chemical bodies, raising the surface tension.

There is little advantage, however, in discussing specific cases, as it is not being suggested here that any one of them represents the processes underlying muscular contraction. It is sufficient for us at present to gain a clear *general* idea of the nature of muscular activity, and to leave the description of specific processes to a day when our knowledge is more adequate. We will proceed, therefore, to consider the general problem, and will make the analogy clearer by employing physiological terms.

(A) The "resting" bubble possesses potential energy: if allowed to "contract" it can do work,

$$A = 4\pi\beta(r_1^2 - r_2^2).$$

(B) The "excited" bubble possesses more potential energy: if allowed to "contract" it can do more work,

$$A' = 4\pi\beta'(r_1^2 - r_2^2),$$

where $\beta'$ is made greater than $\beta$ by some process undefined. If not allowed to "contract," but made to respond "isometrically," the pressure inside the bubble rises from $2\beta/r$ to $2\beta'/r$.

(C) If the "resting" bubble be allowed to contract, doing maximum work, there is a reversible thermal effect, leading to a rise of temperature; if it be made to expand, there is a similar fall of temperature. The heat produced in the contraction is

$$4\pi kT(r_1^2 - r_2^2),$$

where $k$ is the temperature coefficient of the surface tension.

(D) If the "excited" bubble be allowed to contract, there are similar reversible thermal effects, the heat produced on the contraction being

$$4\pi k'T(r_1^2 - r_2^2),$$

where $k'$ is the temperature coefficient of the new surface tension.

*This heat must be added to any produced by the chemical or physical processes leading to the increase of surface tension.*

The analogy with the muscle, therefore, is clear, and we should expect that there would be a reversible thermodynamic evolution of heat equal to

$$\tfrac{1}{2}\alpha T(P_1-P_2)(l_1+l_2)$$

when the excited muscle shortens from length $l_1$ (and tension $P_1$) to length $l_2$ (and tension $P_2$). In this case, however, $\alpha$, the coefficient of thermal expansion, is that of the excited muscle; it would be difficult to devise a direct means of determining this quantity, but there is no reason to doubt its reality. It is presumably negative, as in the unexcited muscle, so that there is then a reversible absorption of heat on contraction, in addition to the transformation of mechanical potential energy into work.

The thermal phenomena described here have no considerable bearing on results *hitherto* obtained on the heat-production of muscles. Most previous work in which the muscles were allowed to shorten over the junctions must anyhow have been vitiated to an unknown degree by differences of temperature along the muscle's length, and conclusions from it are of doubtful value. Most of the more reliable work on the subject was performed on muscles excited isometrically. In the future, however, it will be necessary, as soon as the simpler problem of the isometric contraction has been properly explored, to consider the case of muscles fulfilling their natural, though more complicated, function of shortening; and in that consideration it will be necessary for the investigator to be alive to the difficulties and complications provided by the purely physical thermal effects consequent on the shortening of an extended elastic body.

(b) *Mechanics.*

In considering the mechanics of muscular contraction, the fact that all the potential energy put into a stretched elastic body can be recovered as work *only* if the shortening be infinitely slow is very important. Consider first the case of a muscle passively stretched. If the muscle be *stretched* from a length $l_2$ to a length $l_1$, and if the tension P be required to stretch it to any length, $l$, *then* P *is greater the more rapidly the stretching is carried out.* Consequently, for a given amount of stretching (*i.e.*, for a given final amount of potential energy) the faster the stretching the greater will be the work required and the more wasteful will be the process. Similarly, if the muscle be allowed to shorten from $l_1$ to $l_2$, doing as much work as possible, the tension P exerted at length, $l$, is *less* the more rapidly the muscle is allowed to shorten; consequently, for a given amount of potential energy available, the more rapidly the muscle shortens the smaller is the amount of external work done and the more wasteful the process. What is true of the elastic properties of the unexcited muscle is true also of those of rubber, and in all probability of those of the excited muscle. In that case one very important conclusion follows: *the more slowly a muscle be allowed to contract (in a single twitch) the more work can it be made to do.* This statement should be clearly understood, especially as it may have

a practical application in our study of the heart and other muscles. It should be noted that the contraction considered is supposed to take place between the same geometrical limits in the rapid and in the slow contractions; in the case of the straight muscle it shortens from length $l_1$ to length $l_2$ in either contraction, or in the case of the heart it contracts from volume $v_1$ to volume $v_2$ in either contraction; with this provision, however, in the case of a twitch (or beat) excited by a single given stimulus, *the work done will be greater the slower the contraction is allowed to go on.* The gain in efficiency merely by slowing down the process of shortening may be relatively considerable.*

A further important application is to the case of a muscle contracting under a relatively heavy initial load. When an inactive muscle is loaded heavily, it possesses a considerable amount of potential energy; when the muscle is excited more potential energy is developed as the result of the physiological processes following a stimulus: if the muscle be allowed to shorten, both of these forms of potential energy are available presumably for the production of work, and it would seem natural to subtract the potential energy of the inactive stretched muscle from the total work done, in order to determine how much of the work was done by the muscle in virtue of its own physiological activity. The results of this paper show that such a procedure is not correct, and, indeed, if the initial load be high, may lead to very erroneous results. When a muscle is excited, it contracts rapidly, and when the stretched inactive fibres of the muscle are allowed to shorten rapidly we have shown above that there is a considerable degradation of potential energy into heat, only a fraction of it appearing as external work. Thus the work actually produced by the excited muscle by virtue of its own internal activity is greater, and may under heavy initial loads be considerably greater, than the quantity calculated as described above; while the heat produced by the muscle, by virtue of its internal activity, is less than the heat actually observed, because of the transformation of some of the potential energy into heat when the muscle shortens. If a correct calculation be desired of the work and heat liberated by the unaided internal activity of the muscle, it is necessary to measure:

(*a*) A, the potential energy possessed by the stretched inactive muscle;

(*b*) W, the maximum work obtainable from a mechanical shortening of the inactive muscle *at the same rate of shortening* as obtained in the active twitch.

Then W, and not A, must be subtracted from the work done in the active twitch, in order to get a fair estimate of the share of the work provided by the internal activity of the muscle; while (A—W), expressed in heat units, must be subtracted from the heat-production observed in order to find what amount of this heat is due to the same internal causes.

* This statement must not be misapplied, nor taken from its context.

## (6) The Coefficient of Thermal Expansion of Muscle.

It is interesting to calculate the value of $\alpha$, the coefficient of thermal expansion, from the formula

$$\text{rise of temperature on loading} = -\frac{\alpha T (P_1 - P_2)(l_1 + l_2)}{(\text{mass})(\text{specific heat})(\text{mechanical equivalent})}.$$

On the right side of the formula we can measure everything directly except $\alpha$, while our records enable us to determine the rise of temperature. As a matter of fact, it is necessary, in the records, to separate the reversible thermodynamic production of heat from the irreversible "viscous" one. We have not succeeded in doing this by any rigidly accurate method, but a more or less approximate value can be estimated from the records. The result comes out that $\alpha$ is negative (*i.e.*, the muscle *shortens* on warming) and in size between $10^{-5}$ and $10^{-4}$. Why the muscle has a negative temperature coefficient it is difficult to say. Rubber appears to have the same, and of about the same order of size. It would be of interest to repeat the observation on jellies and on other kinds of rubber or elastic colloidal material. It is striking, however, that the value of $\alpha$ (lying between $10^{-5}$ and $10^{-4}$), calculated for muscle from the experiments described here, agrees in magnitude, though not in sign, with the values given in Tables for a number of materials. For example, in metals $\alpha$ usually lies between $10^{-5}$ and $2 \times 10^{-5}$, gutta-percha is given the value $2 \times 10^{-4}$, glass about $10^{-5}$, and various woods about $5 \times 10^{-5}$.

## (7) Summary.

1. Photographic records, obtained thermo-electrically, are given of the thermal consequences of stretching a muscle, and of releasing a stretched muscle. When a muscle, alive or dead, is passively *stretched*, heat is liberated in large amount at first, but at a rapidly diminishing rate. When a stretched muscle is *released*, the first effect is an absorption of heat, but this is followed, after a short interval, by a production of heat masking the absorption. In a complete cycle of lengthening and shortening the net result is a production of heat, which is greater the greater be the interval between the two processes.

2. These thermo-elastic phenomena are in no way related to the life or visible structure of the muscle, as they are shown by live and dead muscles alike, and, in a modified degree, by a rubber band.

3. The order of size of the thermo-elastic effect may be gathered from the statement that a load of 150 grm., added to a pair of sartorius muscles of *Rana temporaria*, weighing, say, 150 mgr., would raise their temperature by something of the order of 1 to 3 thousandths of a degree, this being a fifth to a half of the rise produced by a strong twitch. These thermo-elastic effects, therefore, are of a size which makes a knowledge of them essential in experimental work on the energetics of muscular activity.

4. The phenomena depend upon the elastic and thermo-elastic properties of the muscle, and may be credited to the simultaneous action of the following two factors :—

(i) The muscle, like catgut, shortens on being warmed ; conversely, the second law of thermodynamics tells us that it will warm on being stretched, and will cool on being released from a stretched state, both processes being "reversible." This explains the initial effects.

(ii) The muscle, like other elastic colloidal jellies, takes some time to reach an equilibrium length on being subjected to a tension ; consequently, on stretching it, *more* work is done, and, on releasing it, *less* work is obtained, than is accounted for by the potential energy existing in it when extended. The balance in either case is liberated irreversibly as heat in the muscle. This explains the later effects.

5. The initial thermal effect—the reversible one, see 4 (i)—enables us to calculate an approximate value for the coefficient of thermal expansion of frog's muscle, and leads to values lying between $-10^{-4}$ and $-10^{-5}$ ; we may assume, therefore, that the sartorius muscle of *Rana temporaria*, subjected to a constant load, shortens by 1 part in something between 10,000 and 100,000 for every 1° C. rise of temperature. The coefficient is of the opposite sign to that for most materials, which lengthen on heating, but is of the same order of size.

6. Experiments are described in which, by means of an inertia system for the determination of the maximum work, the elastic potential energy of the *passively stretched* unstimulated muscle is transformed into work during an elastic contraction occurring at various rates. It is found that the work done is greater the slower is the contraction, but is always considerably less than the potential energy used up. For an infinitely slow contraction, the work done would become equal to the potential energy. The balance of potential energy is used up in irreversible processes, leading to the secondary thermal changes described in 4 (ii) above.

7. It is suggested that the elastic properties of the muscle, leading to the irreversible transformation of work into heat, are the result of its microscopic, ultra-microscopic, or colloidal structure. The relation between tension and extension, as usually found, *i.e.*, leaving the load on till the muscle has settled down to its full extension, is the elastic characteristic of some network ; the spaces between the parts of the network, however, are filled with a viscous fluid, and, when the shape of the muscle is changed, by pulling or releasing it, the viscous fluid has to find a new position inside the network. If the change be very slow indeed, little energy is lost by internal friction ; if, however, the change be rapid, the loss of energy, which increases with the velocity of the fluid, may become large, and lead to a considerable production of heat. The force exerted by the stretched body in such a case is

employed partly in pushing the viscous fluid into its new position inside the network, and partly in doing external work. Naturally, therefore, the external work is less.

8. It is concluded that in order to avoid these complex thermal changes in investigating the heat-production of muscles, it is advisable, whenever possible, to work with rigidly isometric contractions.

9. It is shown that, when an active muscle is allowed to shorten, we may expect to find the thermal changes due simply to shortening superimposed upon those due to the physiological activity (chemical breakdowns, etc.) of the muscle.

10. When a muscle, excited by a single shock, is allowed to shorten from one fixed length to another (or, in the case of the heart, from one fixed volume to another), we may expect to find the external work done greater the slower is the shortening; this may have a practical application in the study of the heart and other muscles.

11. When a muscle is stretched passively by a load, and then excited, the work done is not equal to the potential energy existing initially in the muscle *plus* the work resulting from the internal physiological activity of the muscle. It is less than this by the amount of the potential energy degraded into heat by the viscous processes associated with its rapid change of form. This is of theoretical importance because, in an investigation of the mechanical efficiency of the muscle, it is necessary to determine the work done by the muscle by virtue of its own internal activity, after allowance for work done at the expense of its initial elastic energy; and it is not fair to the muscle to assume that more than a fraction of this potential energy reappears as work.

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# VI.—*The Blood Vascular System of the Tuatara*, Sphenodon punctatus.

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[Plates 6–8.]

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## Introduction.

It is universally admitted that the Tuatara (*Sphenodon punctatus*) occupies a unique place among living Reptiles. By some authorities it is placed in the order Rhynchocephalia, of which it is the sole living representative; others, indeed, have suggested that it should be included in the order Lacertilia, but even in this case it

* The major part of this work was carried out during my tenure of office as Senior Assistant in the Department of Zoology and Comparative Anatomy at University College, London.

is regarded as being one of the least specialised forms. It is, then, a primitive member of the class, and is now only to be found on certain islands off the coast of New Zealand, being so near to extinction that it has been placed under protection by the Government of that country. Any additions to our knowledge of the anatomy of this form therefore seem worthy of being placed on record, particularly when, as will be discussed later, they have some bearing upon its relationship with allied forms.

The animal is one of considerable importance, from the comparative point of view, and yet strangely enough no account of its blood vascular system as a whole has ever been given, either in general or in detail, nor is there, so far as I am aware, a satisfactory description of the general anatomy of the heart. Certain points concerning the arterial system have been described, but others have been left untouched, and the same may be said of the venous system. Indeed, in the case of the latter, although much comparative work has been done along certain lines, there is no good general account of the veins in any member of the order Lacertilia. This being so, it is hoped that the following pages, which contain a fairly full account of the blood vascular system in Sphenodon, will help to fill a noticeable gap in our knowledge of the circulatory system in the Reptilia. In conjunction with Prof. DENDY's account (22) of the intra-cranial vascular system in the same species, it furnishes a more complete account of the blood-vessels than is available even for any of the Lacertilia.

In 1908, Prof. DENDY, F.R.S., suggested to my then fellow-student at King's College, Miss A. W. HILL, B.Sc., that she should work out the vascular system of this important type, and this she proceeded to do. For this purpose, she injected several specimens, and made a number of dissections on the injected and on other uninjected examples. She also made a number of laboratory notes and a series of valuable drawings of her dissections. Before the work was completed, however, Miss HILL left the country, taking with her her notes and drawings. After some years, she found that she would not have an opportunity of completing the work, and Prof. DENDY, in view of the valuable nature and rarity of the material, asked me if I would finish it. This I gladly consented to do, and he placed the original specimens at my disposal. Miss HILL also very generously handed over to me all the notes and drawings she had made, and these, together with the dissections she had left, rendered my task much easier. The drawings have been particularly useful, and I have not hesitated to make full use of them, although in all cases where I have used them I have redrawn them with slight alterations, and this has been indicated by appending thereto both our initials. My own observations were made upon the actual specimens, and the laboratory notes like the drawings served as useful checks.

## MATERIAL.

The material upon which these observations are based is a series of well preserved specimens of *Sphenodon punctatus* in the possession of Prof. DENDY, who had used

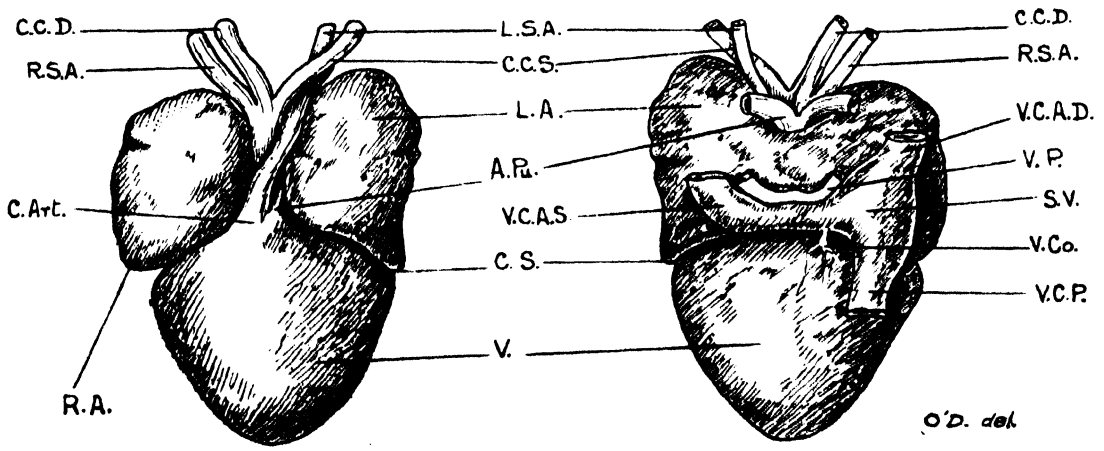
them for his investigations on the intra-cranial vessels (*vide supra*) and on the Pineal apparatus and associated parts of the brain (23). They had been but little touched since they were left, and as they had been carefully preserved, I was enabled to make out practically all the details of the blood vascular system with the exception of one or two unimportant points which are referred to in their appropriate places in the text.

The brains of the injected specimens had been utilised previously, and so, in order to make out accurately the relations of the vessels, particularly the veins of this region, reference was made to series of transverse and longitudinal sections of the heads of late embryos used by HOWES and SWINNERTON in their investigation of the development of the skull (48). They were designated stages R and R–S, and are now in the possession of Prof. DENDY. In this connection I have to thank my former colleague, Dr. K. M. PARKER, of University College, for helping me to make graphical reconstructions of the main vessels of these two stages.

My sincere thanks are due, firstly, to Prof. DENDY for affording me an opportunity of examining such an interesting and valuable species; and, secondly, to Miss A. W. HILL for unreservedly placing in my hands notes and drawings made from dissections which, as I well know, took a great deal of time and exhibited no little skill. Every advantage was taken of this work of Miss HILL, and I am conscious that some of the results set forth below would not have been possible without it.

## THE HEART (text-fig. 1).

In outward appearance the heart of *Sphenodon* is typically reptilian; it is not so elongated as in the Ophidia and many of the Lacertilia, nor so broad as in the




TEXT-FIG. 1.—Sketch of Ventral and Dorsal Surfaces of Heart.

*A.Pu.*, arteria pulmonalis; *C.Art.*, conus arteriosus; *C.C.D.*, carotis communis dextra; *C.C.S.*, carotis communis sinistra; *C.S.*, coronary sulcus; *L.A.*, left atrium; *R.S.A.*, right systemic arch; *S.V.*, sinus venosus; *V.*, ventricle; *V.C.A.D.*, vena cava anterior dextra; *V.C.A.S.*, vena cava anterior sinistra; *V.Co.*, vena coronaria; *V.C.P.*, vena cava posterior; *V.P.*, vena pulmonalis.

Crocodilia. It is about 28 mm. long in an average specimen, and when fairly well distended the atria measure about 30 mm. across. It lies, as in other forms, well forward in the pleuro-peritoneal cavity, practically in the median plane and between the lungs.

*Sinus Venosus.*—The sinus venosus is a well-marked thin-walled sac lying on the dorsal side of the heart just in front of the ventricle; it runs transversely, and the larger part of it is on the right side. It appears to be formed mainly by the confluence of the right anterior caval and the post-caval veins, and their openings are not separated by a semi-lunar ridge, the tuberculum intervenosum, such as we find in the Mammalia. Just to the left of the post-caval vein the coronary vein enters the sinus; it appears as a small but tough cord passing from the sinus across the coronary sulcus on to the wall of the ventricle, as in reptiles generally. To the left of this again, practically in the middle line of the heart, the left anterior caval vein enters the sinus. Outwardly it almost looks as if it were opening into the right atrium, but on slitting the wall of the sinus it will be seen opening into that structure. The aperture leading from the sinus to the atrium is guarded by two distinct valves about 5 mm. long and quite as well developed as in the Amphibia. These sinu-atrial valves lie in the median dorsal wall of the atrium, and run outwards and forwards at an angle of about 75 to the antero-posterior axis of the heart.

*Atrium Dextrum.*—The right atrium is actually larger than the left, but, as it does not pass so far caudally as the latter, it looks somewhat smaller when seen from the ventral surface. From its antero-dorsal edge near the middle line it gives off a small sac-like diverticulum with thin walls, and in two specimens in which the atria were distended with blood, this showed above the diverging bases of the Carotid arteries. It would appear, therefore, as if it was a normal structure, but its function is not obvious. Two portions of the atrium may be distinguished, the main cavity with thin walls and situated mesially and a postero-lateral auricle (auricula cordis) whose walls are thicker and marked internally by interlacing muscular ridges, the musculi pectinati. The two divisions, however, are not sharply defined and merge into one another more gradually than in the mammal.

*Atrium Sinistrum.*—The left atrium is on the whole very similar to the right in general structure and appearance. It is slightly smaller in size and the auricle at its postero-lateral corner overlaps the ventricle more than does the right. The two pulmonary veins open into its postero-mesial walls by a common aperture, which, while not guarded by a definite valve, is partly hidden by a fold of the atrial wall which may function as such.

The two atria from the outside seem to form a single sac, but internally they are completely separated by the septum atriorum. The septum, although slightly thinner in its central region, does not exhibit a distinct fossa ovalis such as we find in the Mammalia.

*Ventriculus.*—The ventricle is a stout-walled sac presenting somewhat the shape of an equilateral triangle when viewed from the ventral surface, and it is about 18 mm. long. It is sharply marked off from the atria by a well-developed coronary sulcus. Its apex is very bluntly rounded, and in one of the specimens examined bore short processes resembling the gubernaculum cordis that BEDDARD has stated to be present generally in the Lacertilia (3). The base of the ventricle is not quite at right angles to the long axis of the heart owing to the fact that the right shoulder is far more rounded off than the left. On the other hand, however, the left auricle overhangs the ventricle more than the right. The dorsal wall of the ventricle is more flattened than the ventral.

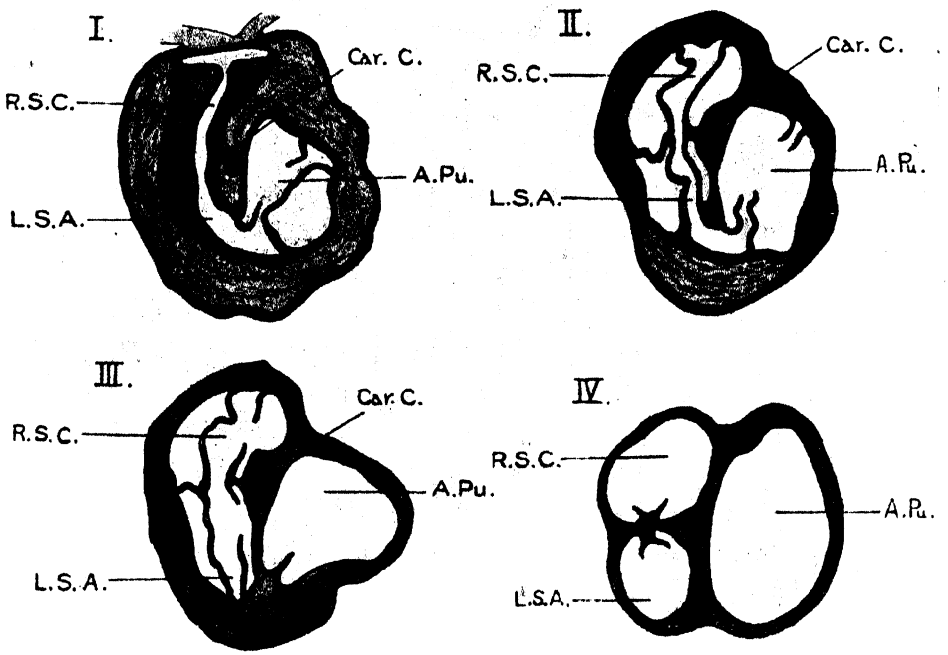
The arterial trunks come off slightly to the right of the middle line from a small anterior projection of the ventricle which, I think, is to be regarded as a remnant of the conus arteriosus for, although it does not bear characteristic conus valves, it nevertheless has valves and constitutes a sort of common trunk from which the arteries arise.

The lumen of the ventricle is quite small owing to the thickness of the wall, which is spongy and composed of an interlacing network of muscular trabeculæ into the interstices of which the blood can penetrate for a considerable distance. The two atria communicate with the ventricle by a common atrio-ventricular aperture situated on the dorsal side of the ventricle at its anterior end. They remain partially separated by an extension of the inter-atrial septum up to the opening which is guarded by a relatively thick flap that separates it from the base of the arterial opening, but does not appear to form a very definite valve. However, the state of preservation of the interior of the heart makes it difficult to speak with certainty on this point.

According to GOODRICH (36A) a small but distinct muscular septum ventriculorum is present in *Sphenodon*. A similar statement is made by GREIL (37), although in neither case is it figured or described in detail. This is a point on which I can make no definite statement as the preservation of the inside of the heart was not good enough to settle the point satisfactorily.

*Trunci Arteriosi* (text-figs. 1 and 2).—The arterial trunks, as has been noted, come off from a slight projection of the ventricle which is probably to be regarded as a remnant of the conus arteriosus. The three trunks, each guarded by a pair of deep semi-lunar valves, present certain points of interest. Viewed externally there appear to be three vessels from the commencement. These are the left systemic trunk, lying ventrally to the right, a right systemico-carotid trunk (*i.e.*, the vessel from which arise the right systemic arch and the two common carotids), lying dorsally and slightly to the right and the pulmonary arch, lying to the left side somewhat dorsally but just visible at the base of the ventricle from the ventral side. A reconstruction revealed the fact that the internal separation of the trunks was not complete, a point that was afterwards verified by careful dissection. At the base the three vessels stand

in open communication with one another and pass backwards a short distance before their common lumen opens into that of the ventricle, and behind this again lies the atrio-ventricular aperture. This is, I think, the portion to be looked upon as the remnant of the conus arteriosus, and although only short is nevertheless quite distinct, and as it bears at its base one pair of semi-lunar valves obviously cannot be considered as part of the ventricle.




TEXT-FIG. 2.—Outline sketches of four sections through the Main Arterial Trunks, drawn with a Zeiss Meyer camera lucida and stand.

I. At the level where all three arterial trunks are in open communication and posterior to the valves of the right systemico-carotid and left systemic trunks (slide 14, No. 5).

II. At the level where all three trunks are still in communication but the valves in right systemico-carotid and left systemic trunks are fully developed (slide 17, No. 1).

III. At level where main septum completely separates the pulmonary artery but the right systemico-carotid and left systemic are in communication (slide 19, No. 8).

IV. At level where all three trunks are completely separated; at front limit of valves and anterior to the cardiac cartilage (slide 22, No. 10).

*A.Pu.*, arteria pulmonalis; *Car.C.*, cardiac cartilage; *L.S.A.*, left systemic arch; *R.S.C.*, right systemico-carotid.

## THE ARTERIAL SYSTEM.

The groundwork of our modern knowledge of the arterial system in the Saurians was laid by CORTI, in 1847, in his detailed account, 'De Systemate Vasorum *Psammosauri Grisei*,' in which he also gives a short account of previous work. This was followed ten years later by a splendid paper by RATHKE (66), dealing with the

aortic roots in general and based upon an examination of 55 different species of Lacertilia and Crocodilia. He did not, however, examine *Sphenodon*. Since this time considerable additions to our comparative knowledge of various parts of the system have been made. In the first place, RATHKE (67) and HOCHSTETTER (44) have described the main gut arteries in many species. Secondly, ZUCKERKANDL (82, 83, and 84) has treated the arteries of the fore and hind limbs in a series of Amniotes, including Lacertilians; and, thirdly, BEDDARD (3, 4, 5, and 7) has investigated the relationship of various arteries in a number of different forms.

As far as *Sphenodon* itself is concerned, it has only been very incompletely studied. VAN BEMMELEN (10), in 1887, wrote a description of the neck region, in which, although mainly concerned with the nerves and their primitive relations to the branchial arches, certain of the neck arteries are accurately described. The main limb arteries were examined by ZUCKERKANDL (*loc. cit.*), and BEDDARD (7) dealt with the main arteries coming from the anterior part of the dorsal aorta. The visceral arteries were first treated, but in a very brief manner, by KLAATSCH (50), and this work was later extended by HOCHSTETTER (44). Finally, DENDY (22), from the same specimens he placed at my disposal, described in detail the intra-cranial arteries, which are therefore omitted here, save that their connections with the extra-cranial vessels are pointed out.

The presence of semilunar valves at the bases of the three arterial trunks and the points of origin of these vessels have already been dealt with. They pass forward together on the ventral side between the median walls of the atria, rotating slowly in a clockwise direction as they do so. Thus, the left systemic trunk starts from the conus ventrally and to the right of the group, and leaves the anterior end of the heart on the left side dorsal to the carotid arch. The pulmonary trunk commences on the left side and leaves dorsally; the right systemico-carotid trunk arises on the right dorsal and finishes on the right ventral side. Thus it will be seen that, while there is a certain amount of twisting, it is not as great as in other Reptiles.

The arterial system is best dealt with by describing the course and distribution of the three arterial arches arising from the three trunks, starting with the anterior pair.

### *The Carotid Arch* (Plate 7, figs. 2 and 3).

The two common carotid arteries take origin together practically in the middle line, from the same point on the right systemic arch just as it commences to bend outwards over the trachea. There is thus no joint trunk or carotis primaria for these two vessels.

According to RATHKE (66, p. 62), two different arrangements are met with in the Lacertilia; in the one the two common carotids come off separately from the right systemic arch, and in the other they come off from a common carotis primaria, which in its turn arises from the right systemic. Even when present, the carotis primaria varies considerably in development, reaching its maximum in the *Varanidæ*, where it

is quite long, and becoming so small in certain groups, including the *Lacertidæ*, that it may readily be overlooked. The two vessels in *Sphenodon* certainly have one common opening into the right systemic arch, but they do not run together until this point, and so it is not possible to speak of a carotis primaria in this form. It is difficult to say whether this approximation to the condition of the *Lacertidæ* is indicative of phylogenetic relationship. The point in itself cannot be pressed too far, as a similar range of differences occurs in the Ophidia; in *Boa*, for example, the two common carotids come off separately, while in *Tropidonotus* a well-developed carotis primaria is present (58).

The two common carotids and their branches in *Sphenodon* pursue almost identical courses on the two sides of the neck and head, save perhaps in some of their smaller unimportant twigs, so that the description given for one side will apply equally well to the other.

*The Carotis Communis* (Rathke, Corti) (Plate 7, figs. 2 and 3, text-figs. 6 and 7).—The common carotid runs sharply outwards and slightly forwards round the trachea to the latero-ventral wall of the œsophagus, where it divides into two branches, the external carotid (B) and the internal carotid (C). Close to its origin it gives off a small vessel (A). Rathke has noticed three different conditions of the common carotid in the Lacertilia in general: (1) In the *Varanidæ*, where the heart lies a long way back from the head, not only is a carotis primaria developed, but the common carotid runs a good way up the neck before dividing into external and internal branches. A ductus caroticus joining the carotid to the systemic arch is not present. (2) Similarly in the *Chamæleontidæ* no ductus caroticus is present save in *Chamæleon planiceps*, where it is still to be found on each side as a very fine vessel visible only with a hand lens. (3) The third group includes most of the remaining forms where the heart, as a general rule, is not far back from the head, and in these a ductus caroticus is present. The condition in *Sphenodon* is very similar to that in the *Lacertidæ*.

A. *Arteria pericardialis* ('Arterie für das Pericard.,' v. Bemmelen (10)) is a small vessel going to the pericardium.

B. *Carotis externa* (v. Bemmelen; Ramus trachealicus, Corti; 'Kehl-Zungenast des Carotidenbogens,' Rathke) (Plate 7, fig. 3, text-fig. 7).—The external carotid is a fairly small artery arising from the outer wall of the common carotid, and it runs forward close to the œsophageal wall and gradually outwards, keeping laterad of most of the nerves of the neck. It is a continuation forward of the ventral aorta of the embryo. With the exception of a small thyroid branch (B. I), it remains a single trunk up to the hyoid region. Just after crossing the outer surface of the ceratohyal it is itself crossed ventrally by the hyo-maxillary branch of the twelfth cranial nerve, the largest nerve in this region, and then it immediately divides into two main

branches, the hyomandibular (B. II) and the superficial pterygoid (B. III), which supply the various muscles and tissues of the mental region and the postero-lateral part of the jaws.

According to RATHKE, the external carotid in Lacertilians arises very close to the "Kopfast," *i.e.*, the internal carotid, after the place where it receives the ductus caroticus, but in certain forms, including *Lacerta ocellata* and *L. agilis*, these two points are situated some distance apart. The condition in *Sphenodon* most nearly approaches that found in the *Lacertidæ*.

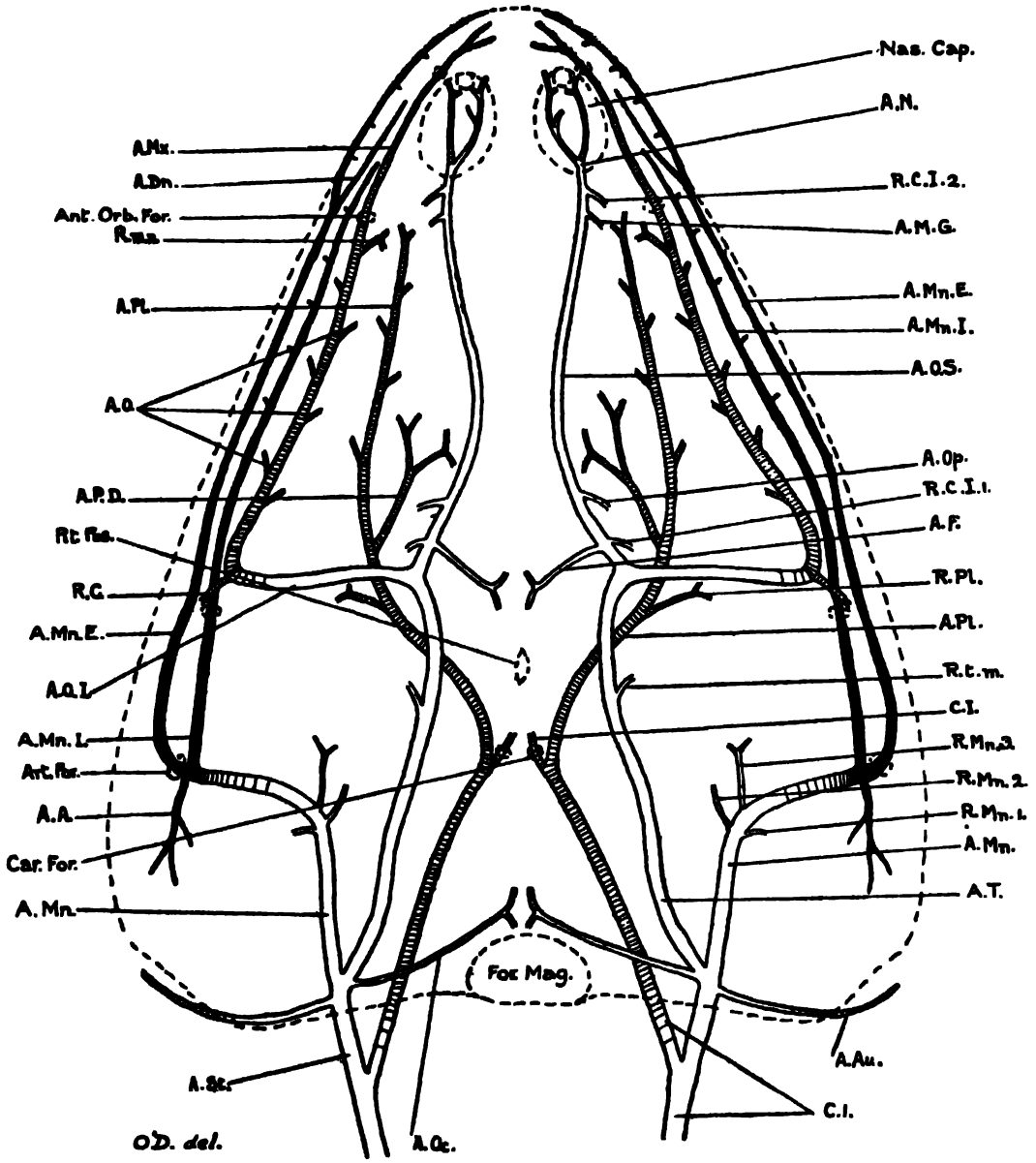
B. I. *Arteria thyreoidea superior* (v. BEMMELEN, 'Thymusdrusen Ast,' RATHKE). —The thyroid artery is a small vessel coming off from the external carotid immediately after the origin of the latter. It runs forwards and inwards, entering the lateral lobe of the thyroid gland.

RATHKE states that in the Lacertilia this branch may sometimes come from the external carotid and sometimes from the common carotid, but he erroneously calls it a thymus branch, as he had previously made the mistake of identifying the thyroid as a thymus gland. VAN BEMMELEN (10) gives two figures of this vessel in *Sphenodon*: in Plate I, fig. 1, it is depicted as arising from the common carotid, which, as far as my observations go, is incorrect; but in Plate I, fig. 6, he shows it correctly coming from the external carotid. The first of these figures, although very good in many ways, somewhat distorts the arteries in order to display the nerves, with which the author was more particularly concerned, and this may account for the inaccuracy.

B. II. *Arteria hyomandibularis* (A. sub-mentalis superficialis, CORTI (text-fig. 3)).—This is the inner and slightly larger of the two branches into which the external carotid divides. It gives off a glossopharyngeal branch (II. $\alpha$) shortly after its origin, and then runs forwards along the inner border of the hyoideus muscle to its anterior end. Here it passes along the inner border of the end of the anterior cornu of the hyoid and then divides into two main trunks, a submandibular (II. $\beta$) and a genioglossal (II. $\gamma$).

B. II. $\alpha$. *Arteria glossopharyngeus.*—The glossopharyngeal artery arises from the base of the hyomandibular and passes dorsal to the hypoglossal nerve to take up a position on its inner side. It accompanies this nerve forward, giving branches to the hyomaxillaris muscle, and on into the genioglossus muscle, to which it also gives branches. It can be followed along the outer ventral border of this muscle almost to its anterior end.

B. II. $\beta$. *Arteria sub-mandibularis* (text-fig. 7).—This is a well-marked vessel, situated on the outer ventral surface of the hyomandibularis muscle and running forward on its right to its anterior end at the symphysis menti.




TEXT FIG. 3.—Diagram of the Main Arteries of the Head, exclusive of the Lower Jaw, viewed from above. Ventral arteries solid, dorsal arteries clear, and intermediate arteries shaded.

*A.A.*, arteria articularis; *A.Au.*, arteria auricularis; *A.Dn.*, arteria dentalis; *A.F.*, arteria frontalis; *A.M.G.*, arteria musculo-glandularis; *A.Mn.*, arteria mandibularis; *A.Mn.E.*, arteria mandibularis externa; *A.Mn.I.*, arteria mandibularis interna; *A.Mx.*, arteria maxillaris; *A.N.*, arteria nasalis; *Ant.Orb.For.*, anterior orbital foramen; *A.O.*, arteriæ orbitales; *A.Oc.*, arteria occipitalis; *A.O.I.*, arteria orbitalis inferior; *A.Op.*, arteria ophthalmica; *A.O.S.*, arteria orbitalis superior; *A.P.D.*, arteria palatina dorsalis; *A.Pl.*, arteria palatina; *Art.For.*, articular foramen; *A.St.*, arteria stapedialis; *A.T.*, arteria temporalis; *Car.For.*, carotid foramen; *C.T.*, carotis interna; *For.Mag.*, foramen magnum; *Nas.Cap.*, nasal capsule; *Pit.Fos.*, pituitary fossa; *R.C.*, ramus coronoideus; *R.C.I.* 1 and 2, rami musculares of the arteria orbitalis superior; *R.m.n.*, ramus membranæ nictitantis; *R.Mn.* 1, 2, and 3, rami musculares of the arteria mandibularis; *R.Pl.*, ramus muscularis of the arteria palatina; *R.t.m.*, ramus temporo-masseteria.

It gives off branches to the adjacent musculature throughout the whole of its course, the largest of which are the following :—

II. $\beta$. i. The *Ramus musculo-mandibularis* is a large artery, passing outwards and upwards towards the inner surface of the mandible and dividing into two main branches, which enter the platysma muscle.

$\beta$. i. a. A *Ramus ventralis*, that is distributed to the main mass of the posterior part of the platysma muscle.

$\beta$. i. b. A *Ramus dorsalis*, that sends twigs into the deeper layers of the platysma and then runs along the inner surface of the mandible.

II. $\beta$. ii. The *Ramus muscularis* 1, a small artery that turns inwards and branches in the substance of the hyomaxillary muscle.

II. $\beta$. iii and iv. *Rami musculares* 2 and 3 also pass inwards but are distributed to the superficial and deeper layers of the genio-hyoideus muscle.

II. $\beta$. v–viii. *Rami musculares* 4–7, are distributed to the anterior portions of the platysma muscle.

II. $\gamma$. *Arteria genioglossa.*—The genioglossal artery leaves the main trunk at the level of the larynx and passes inwards and forwards along the side of the genioglossus muscle, to which it gives branches, to end just behind the mandibular symphysis.

B. III. *Arteria pterygoideus superficialis* (Plate 7, fig. 3, text-fig. 7).—The superficial pterygoid artery leaves the external carotid just after this vessel is crossed by the hypoglossal nerve and passes outwards. It gives off small branches to the ventral surface of the internal pterygoid muscle, along which it runs forwards, and at the anterior end of that muscle gives off one or two small branches to its dorsal surface. It is continued forward, branching repeatedly in the strip of subcutaneous tissue that lies between the hyomandibular muscle and the inner aspect of the mandible, and finally ends somewhere in the region of the anterior end of the hyoid (Processus entoglossus of OSAWA (62)).

C. *Carotis interna* (last part of Carotis communis, CORTI ; 'Kopfast des Carotidenbogens,' RATHKE) (Plate 7, fig. 3, text-fig. 3).—The internal carotid artery is a large artery, at least twice the diameter of the external carotid and, from the point of origin of the external carotid, it passes outwards and very slightly forwards over the ventral œsophageal wall. A little way along it bears on its posterior wall a small nodule, the carotid gland, and just beyond this receives the ductus caroticus (C. I). At this point it turns sharply forward, passing along the side of the œosophagus and is now, of course, the continuation forward of the old dorsal aorta of the embryo. Between the carotid gland and the point of entry of the ductus caroticus, the nervus laryngeus superior, a branch of the Vagus, loops around the internal carotid and runs forward up

the neck. According to VAN BEMMELEN (10) the carotid gland communicates with the second thymus gland by a very fine strand of tissue. Unfortunately owing to the condition of the specimens I examined I have not been able to verify this observation.

A fairly large lymphatic vessel appears to enter the internal carotid on its ventral side at the same level as the ductus caroticus. This lymphatic trunk runs along the outer side of the internal carotid and alongside the vagus, passing under the internal jugular vein, and it is dilated just where it enters the carotid. The internal carotid continues forwards immediately below the second thymus and then outside the first thymus, at the anterior end of which it passes below the trunk of the hypoglossal nerve just as this is bending round towards the mental region. The artery then goes on, passing in succession superficially to the cervical sympathic nerve, the glosso-pharyngeal just as this curves outwards on the œsophageal wall, the internal jugular vein, and the vagus nerve. During this part of its course it gives off small twigs to the adjacent neck muscles, *e.g.*, the cucullaris, parieto-mandibularis, longissimus, etc.

Immediately after passing the vagus it gives off a very large trunk, the stapedial (B. II), and itself turns downwards and slightly inwards to run forward first on the lateral wall of the quadrate, then below the auditory capsule and finally on the base of the skull. Beneath the basisphenoid bone it gives off a fair-sized branch, the palatine (B. III), and then enters the cranial wall through the carotid foramen in the basisphenoid. It mounts in the wall of the sella turcica laterad of the hypophysis, to which it gives a small twig, and then in the substance of the cranial wall, which is here membranous, to a point just below the exit of the oculo-motor nerve and then turns inwards, becoming completely intra-cranial, to the latero-ventral wall of the brain. Here on the ventral surface of the crus cerebri it divides into an anterior (B. IV) and a posterior (B. V) branch. The distribution of these branches has already been worked out very carefully and fully by DENDY on the same specimens employed here, and is described in his paper on "The Intracranial Vascular System of Sphenodon" (22) and so need not be repeated.

C. I. *Ductus caroticus.* (Absteigender Schenkel des Carotidenbogens, RATHKE; junction of the Carotid and Aortic Arches, VAN BEMMELEN) (Plate 7, fig. 3, text-figs. 6 and 7).—This is a well-marked vessel of about the same calibre as the internal carotid itself. It runs from the postero-dorsal wall of the carotid, where it turns forwards immediately beyond the carotid gland, to the outer wall of the systemic arch a short distance in front of the ductus Botalli, thus putting the aortic and carotid arches in free communication with one another. Slightly nearer the systemic arch it gives off a moderate-sized branch (I. α), the muscularis cervicis. Some confusion exists in the

nomenclature of this vessel, as it has been termed the ductus Botalli by BEDDARD (3, 7 and 8) in certain lizards, whereas it is more properly called the ductus caroticus, as it was first named by BRANDT (17). This matter, together with the distribution of the two ductus in Reptilia, I have dealt with more fully previously (60), and it is only necessary to call attention to one or two points therein mentioned. It is not found in the *Varanidæ* nor as an open vessel in the *Gekonidæ*. Although present in many other Lacertilians, it is very often reduced in diameter or even a solid strand, a ligamentum caroticum, but in none of these is it less specialised than in *Sphenodon*.

The presence of both ductus caroticus and ductus arteriosus (Botalli) is a point of considerable importance. As they are to be found in the embryos of the Amniota, in adult Urodele Amphibia according to BOAS* (12, 13 and 14) and FRITSCH (28), and in the very young frog at the time of metamorphosis, we may justifiably conclude that the presence of both vessels in the higher forms indicates the retention of a fairly primitive condition. Indeed we may say, as has been pointed out elsewhere (60), "In this particular, as far as is known, *Sphenodon* is more primitive than any other living reptile."

C. I. *α*. *Arteria muscularis cervicis* (VAN BEMMELEN).—The cervico-muscular artery is a vessel running dorsally to supply the muscles in the region of the nape of the neck and the shoulders. According to VAN BEMMELEN it also gives off branches to the thymus glands, but I have not been able to verify this.

C. II. *Arteria stapedialis* (Carotis externa, CORTI; A. facialis, RATHKE) (Plate 7, fig. 2, text-fig. 3).—As has been noted already, the stapedial artery leaves the carotid just after this passes the Vagus nerve. It is a large trunk, considerably larger indeed than the continuation of the internal carotid, and its ramifications cover the whole of the temporal, orbital and a large part of the maxillo-mandibular region. The stapedial runs forward on the median side of the quadrate bone, between it and the cranial wall and then immediately ventrad of the columella auris. Just beyond the columella it gives off a small auricular twig (II. *α*) and then divides into two large almost equi-sized trunks, the temporal (II. *β*) and the mandibular (II. *γ*). Before it divides, the stapedial artery, which was ventral to the vena capitis lateralis, passes laterally around this vein so that the bifurcation takes place dorso-lateral to it.

C. II. *α*. *Arteria auricularis* (CORTI).—The auricular artery is a small vessel

* In as far as this statement refers to *Triton* and *Salamandra*, I have been able to confirm it by dissection.

which follows the chorda tympani along the posterior wall of the tympanic cavity. It passes along the posterior border of the second epibranchial, giving off in the tympanic region a small posterior tympanic artery which perhaps anastomoses with the external carotid artery.

C. II. β. *Arteria temporalis* (A. facialis, RATHKE) (Plate 7, fig. 2, text-fig. 3).—The temporal artery is slightly the larger of the two branches into which the stapedial divides. After giving off a small occipital branch (β. i) it passes upwards and forwards along the upper border of the cranium between the fascia of the longissimus muscle, to curve forward over the external pterygoid muscle. It gives off a small branch to the temporo-masseter muscle (β. ii) and at the anterior border of the pterygoid it splits into two main trunks, the supra-orbital (β. iii) and the infra-orbital (β. iv) arteries.

II. β. i. *Arteria occipitalis.*—The occipital artery is a small vessel running upwards in the longissimus muscle, to which it gives branches, on the side of the parietal bone. It divides into anterior and posterior branches.

II. β. ii. *Ramus temporo-masseteris.*—This is a small twig, supplying the similarly named muscle.

II. β. iii. *Arteria orbitalis superior* (RATHKE; A. orbito nasalis, GAUPP) (Plate 7, fig. 2, text-fig. 3).—The supra-orbital artery is a large one, continuing more or less in the line of the temporal. At the posterior end of the orbit it gives off three branches: one (iii. a) to the region of the frontal bone, another (iii. b) to the retractor muscle of the eye, and the third (iii. c), which runs outwards to the back of the eyeball, and is distributed to its muscles. The main trunk then continues forward in the dorsal wall of the orbit, and then penetrates the cartilaginous inter-nasal septum. In this it runs below the ophthalmic nerve, and leaves the septum again to re-enter the orbit at its anterior end. Here two branches are given off, one (iii. d) to the glands and muscles, and another (iii. e) to the inferior oblique muscle, and the artery goes on as the nasal (iii. f) into the olfactory capsule.

II. β. iii. a. *Arteria frontalis.*—The frontal artery is a small branch arising just behind the orbit. It runs upwards to the frontal bone, where it divides into an anterior and a posterior branch, supplying the superficial tissue.

II. β. iii. b. *Ramus muscularis* 1.—A fairly small artery, arising near the frontal, runs to the proximal part of the retractor bulbi muscle of the eye.

II. β. iii. c. *Arteria ophthalmica* (Plate 8, fig. 10).—The ophthalmic is a somewhat larger artery, running downwards on to the back

of the eyeball. It is distributed to the muscles of the eye as follows :—

c. 1. A branch to the posterior rectus.
c. 2. A branch to the anterior part of the retractor bulbi.
c. 3. A branch to the superior rectus.
c. 4. A branch to the back of the eye.
c. 5. A branch to the anterior rectus.
c. 6. A branch to the inferior rectus.

II. β. iii. d. *Arteria musculo-glandularis.*—This runs downwards, giving off a backwardly directed twig to the sclerotic coat of the eyeball. Continuing, it passes through the superior oblique muscle, supplying it with a twig, and on into the Harderian gland, in which it breaks up.

II. β. iii. e. *Ramus muscularis* 2 runs straight downward, and is distributed to the inferior oblique muscle.

II. β iii. f. *Arteria nasalis.*—The remaining part of the supra-orbital may be termed the nasal artery, since it enters the olfactory capsule and is distributed mainly to the olfactory organ, although its terminal branches end in the subcutaneous tissue of the snout. On entering the capsule it divides into two main twigs, the superior and inferior nasal arteries. These run in the floor and roof of the nasal cavity respectively, supplying the mucous membrane and the end of the snout, as indicated above.

II. β. iv. *Arteria orbitalis inferior* (A. dentalis superior, RATHKE) (Plate 7, fig. 2, text-fig. 3).—The infra-orbital artery leaves the temporal at the postero-dorsal corner of the orbit, turning sharply downwards in its hinder membranous wall. In then runs on in the floor of the orbit, accompanying the infra-orbital branch of the trigeminal nerve. In this part of its course it gives off the coronoid (β. iv. a) branch and others to the surrounding tissues (β. iv. b) and nictitating membrane (β. iv. c). At the front end of the orbit it enters the maxilla through the anterior orbital foramen, and so becomes the maxillary artery (β. iv. d).

II. β. iv. a. *Ramus coronoideus.*—This vessel is given off from the infra-orbital just as it turns to run forward in the floor of the orbit. It breaks up into small branches, distributed to the tissue in the coronoid region.

II. β. iv. b. *Arteriæ orbitales.*—While passing through the orbit, the infra-orbital artery gives off small vessels to the adjacent tissue.

II. β. iv. c. *Ramus membranæ nictitantis.*—At the anterior end of the

orbit the infra-orbital artery sends a branch upwards, to supply the nictitating membrane.

II. $\beta$. iv. d. *Arteria maxillaris* (RATHKE) (text-fig. 3).—The maxillary artery is really the continuation of the infra-orbital, but deserving of a special name, since it enters the substance of the maxilla by the anterior orbital foramen. It runs forward in the jaw for some way, and finally leaves it, by a foramen at the anterior end of the maxilla, just beneath the external naris, to terminate in the subcutaneous tissues of the snout. While running in the maxilla it gives off four or five small branches, which pass outwards through tiny foramina to the subcutaneous tissues of the upper lip.

C. II. $\gamma$. *Arteria mandibularis* (RATHKE) (Plate 7, fig. 2, text-fig. 3).—The mandibular artery passes forwards from the stapedialis along the cranial wall until it reaches a point just below the roots of the trigeminal nerve, when it turns outwards and passes between the internal pterygoid and temporo-masseter muscles, accompanying the mandibular branch of the fifth nerve. Small branches are given off to the temporo-masseter muscle ($\gamma$. i and $\gamma$. iii) and the internal pterygoid muscle ($\gamma$. ii). At the level of the mandible the mandibular artery divides into an internal ($\gamma$. iv) and an external branch ($\gamma$. v).

II. $\gamma$. i. *Ramus muscularis* 1.—A small artery leaves the main trunk just before it reaches the level of the roots of the fifth nerve. It passes outwards, and is distributed to the temporo-masseter muscle in that region.

II. $\gamma$. ii. *Ramus muscularis* 2.—A small branch is given off immediately before the mandibular takes up its position alongside the corresponding branch of the fifth nerve. This supplies the internal pterygoid muscle.

II. $\gamma$. iii. *Ramus muscularis* 3.—Another branch, arising shortly after the former, runs forward to the anterior part of the temporo-masseter muscle.

II. $\gamma$. iv. *Arteria mandibularis interna*.—The inner fork of the mandibular artery passes forward along the inner aspect of the mandible to the coronoid region. Here it enters the bone through a foramen on the inner side of the coronoid bone and continues forward, first in the bone itself, but soon in the deep Meckelian groove. Several twigs leave it during its course, and pass outward to the subcutaneous tissue of the lower jaw.

II. $\gamma$. v. *Arteria mandibularis externa* (Plate 7, fig. 2, text-fig. 3).—After parting from the foregoing, this artery gives off a small articular branch (v. a), and then passes through the mandible, *vid* the articular foramen, to the outer aspect of the jaw, where it turns sharply

forwards. In the dentary region it gives off a small dentary branch (v. b), and then goes on to supply the remaining part of the lower jaw up to the symphysis, and also sends twigs to the subcutaneous tissue of the lower lip.

II. $\gamma$. v. a. *Arteria articularis* is a small vessel running backwards to the tissues in the articular region.

II. $\gamma$. v. b. *Arteria dentalis* is a small branch from the external mandibular that enters the substance of the mandible in the dentary region. It runs forward below the teeth, to which it sends shoots, and it also gives off a few twigs, which pass through the bone to the outside.

C. III. *Arteria palatina* (text-fig. 3).—As has been indicated above, the palatine artery arises from the internal carotid beneath the basisphenoid bone just before the latter artery enters the carotid foramen. At first the palatine runs near the middle line, accompanying the third cranial nerve, and some distance along gives off a muscle branch (III. $\alpha$), by which time it has turned slightly outwards. At the level of the sub-orbital foramen, a dorsal palatine branch (III. $\beta$) is given off. The main trunk runs forward beneath the palatine bone, giving off numerous branches to the sub-mucosa of the roof of the mouth, and finally breaks up in the sub-nasal region.

C. III. $\alpha$. *Ramus muscularis.*—This branch of the palatine artery passes outwards and forwards, to be distributed to the posterior wall of the orbit, and supplying a well-marked twig to the retractor bulbi muscle.

C. III. $\beta$. *Arteria palatina dorsalis.*—This takes a course forward dorsal to the palatine bone, and breaks up into a number of vessels, supplying the tissue in the vicinity.

C. IV. *Ramus cranialis* of the internal carotid.

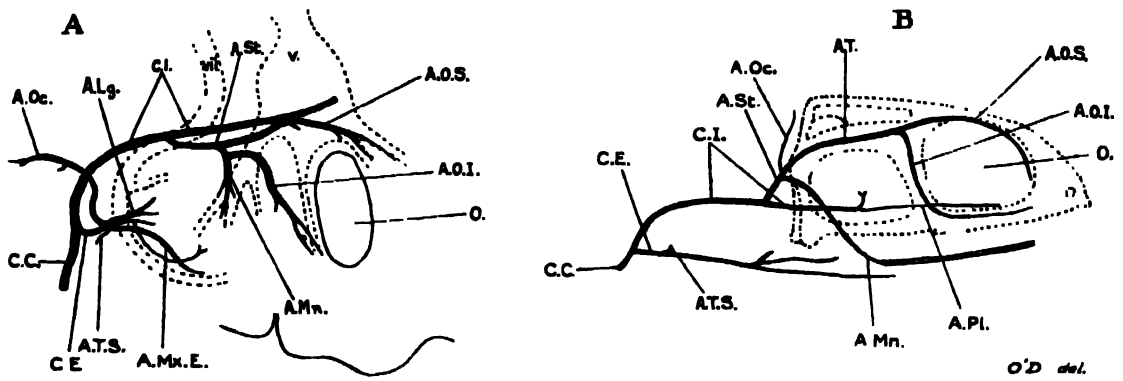
C. V. *Ramus caudalis* of the internal carotid.

These two branches forming the termination of the internal carotid artery and their intra-cranial distribution have already been fully described by DENDY (22), and are only mentioned here for the sake of completeness.

*The Distribution of the Carotid Arteries* (text-fig. 4).

It seems advisable at this point to call attention to the difference in the territories supplied by the internal and external carotid arteries in *Sphenodon* and the Mammalia respectively. In the mammal, the internal carotid is usually solely intra-cranial in its distribution, while all the remaining parts of the face and jaws are supplied by branches of the external carotid. The condition in *Sphenodon* is very different, however, for here the internal carotid serves not only the brain, but also the whole of the palate, face, and jaws, while the external carotid is relatively a much smaller and

less important vessel, and is concerned mainly with the musculature of the lower jaw. At first sight this striking dissimilarity appears to indicate a fundamental difference between the two conditions, but the reason for it becomes clear in the light of TANDLER'S account (75) of the development of the carotid arteries in mammals. In the mammalian embryo we find the vessels arranged very much as in the reptile; indeed, it is interesting to notice that the arrangement in the 14 mm. human embryo according to EVANS (25) is essentially similar to that in *Sphenodon* and also to that in *Iguana tuberculata* according to RATHKE (67). The actual spatial relations are not the same, of course, owing to the very different proportions of the parts of the




TEXT-FIG. 4.—Diagrams for the comparison of the Internal and External Carotids of the Human Embryo and in *Sphenodon*.

A. Graphic reconstruction of the head arteries in a human embryo measuring 14 mm. Adapted from EVANS (25). B. Diagrammatic representation of the carotids in the adult *Sphenodon*. Approximate position of the skull indicated by dotted lines.

*A.Lg.*, arteria lingualis; *A.Mn.*, arteria mandibularis; *A.Mx.E.*, arteria maxillaris externa; *A.O.C.*, arteria occipitalis; *A.O.I.*, arteria orbitalis inferior; *A.O.S.*, arteria orbitalis superior; *A.Pl.*, arteria palatina; *A.St.*, arteria stapedialis; *A.T.S.*, arteria thyreoidea superior; *C.C.*, carotis communis; *C.E.*, carotis externa; *C.I.*, carotis interna; *O.*, orbit; v and vii, primordia of the fifth and seventh cranial nerves.

head involved, the eye in *Sphenodon* being well in front of the brain, and the brain in the mammalian embryo being relatively larger. The most noticeable points of difference are that in *Sphenodon* the mandibularis artery arises nearer to the origin of the stapedialis (a change perhaps necessitated by the anterior position of the eye). The internal carotid gives off a palatine artery just before entering the skull, and the occipital artery is a branch of the temporal and not of the external carotid (this last difference, however, is not shown by *Varanus griseus*). Although the details of the branches of the external carotid then vary somewhat, the region supplied is essentially the same in each case.

In the mammalia in general an anastomosis is formed during the course of development between the stapedial artery and a branch of the external carotid, and with the later disappearance of the stapedial artery all its branches become transferred to the external carotid. Hence the difference between the regions supplied by the vessels in *Sphenodon* and mammals. The arteria stapedialis appears to persist in

certain mammals, but even when it does, owing to the anastomosis, it gives up to the external carotid the mandibular artery as in the rat (TANDLER, 75), and in addition the infra-orbital artery in the case of the bat (GROSSER, 38).

*The Systemic Arch* (Plate 6, fig. 1, text-fig. 6).

As mentioned previously, HOCHSTETTER (44) dealt with *Sphenodon* in the course of a comparative account of the arteries of the alimentary canal. It is noteworthy that he considers the relation of these vessels in *Sphenodon* to be primitive and one from which other Lacertilian arrangements can be derived. BEDDARD (7) has furnished an account of the origin of the vessels coming from the systemic arch and the anterior part of the aorta. On the whole, the present work confirms that of these two writers. and also that of ZUCKERKANDL (82, 83, and 84) on the limb arteries. In spite of these works, no complete account of the systemic and aortic branches has yet been given.

The two systemic arches come off separately from the ventricle. The left systemic arch arises as the right ventral vessel of the three coming from the ventricle and it passes in a slight spiral twist over to the left, becoming more dorsal as it does so. The right systemico-carotid is slightly the largest and the most dorsal of the three trunks; it passes slightly to the left and becomes more ventral. As has been pointed out before, it gives off the carotids at the level of the anterior end of the atria, after which it becomes the systemic arch. From this point the courses of the two systemic arches are the same. Each vessel passes laterally and slightly forwards out on to the wall of the œsophagus; at the side of this it gives off a short branch, the anterior œsophageal (A), and exhibits a slight swelling of its wall, the œsophageal gland (VAN BEMMELEN, 10). Here the vessel turns downwards and inwards on to the dorsal wall of the œsophagus. It almost immediately receives on its anterior wall the ductus caroticus, and a short way beyond that the ductus arteriosus (ductus Botalli). The ductus arteriosus is a small vessel connecting the pulmonary and systemic arches. The systemic arches pass backwards and inwards and finally unite in the middle line to form the dorsal aorta. Dorsally to this junction the two sub-clavian arteries (B) are given off. Close examination shows, as BEDDARD (7) has pointed out, that the two arteries actually arise from the right systemic, but just at the point where it joins the left. In *Chamæleon*, according to MACKAY (54), the two sub-clavians arise well up on the right systemic arch. From its point of origin the dorsal aorta runs backwards in quite a normal way, giving off a number of branches (C–N). At the posterior end of the cœlom it passes on into the hæmal canal and as the caudal artery continues right down the tail.

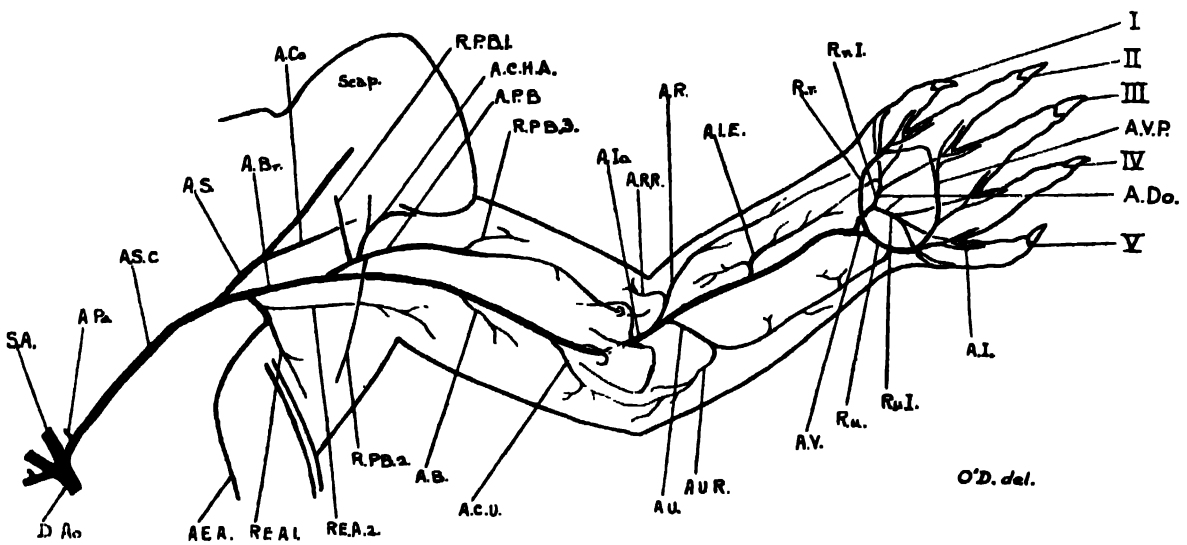
A. *Arteria œsophagea anterior.*—This is a small vessel running forwards up the side of the œsophagus from the systemic arch.

B. *Arteria subclavia* (CORTI) (text-fig. 6).—The origin of the sub-clavian artery has been described above. It passes outwards, giving off three branches

(B. I–III) and enters the arm, where it is termed the brachial artery. In its course along the arm to the entepicondylar foramen it gives off an arteria profunda brachii (B. IV) and other branches (B. V and VI). After passing through the foramen it issues into the muscles of the forearm, where it is termed the arteria interossea, and on its way to the carpus gives off branches (B. VII–X). It finally splits into two terminal branches (B. XI and XII) on the extensor surface of the metatarsals of the fore foot.

B. I. *Arteria parietalis.*—The first vessel is given off by the sub-clavian close to its origin, and is a parietal artery similar to those coming off from the aorta.

B. II. *Arteria scapularis* (Corti).—This is a fairly large vessel going to the shoulder girdle. Its main stem forms a supra-scapular trunk, but it also




Text-fig. 5.—Diagram of the Arteries of the Left Fore-limb from the Flexor Side.

*A.B.*, arteria bicipitalis; *A.Br.*, arteria brachialis; *A.C.H.A.*, arteria circumflexa humeri anterior; *A.Co.*, arteria coracoidea; *A.C.U.*, arteria collateralis ulnaris; *A.Do.*, arcus dorsalis; *A.E.A.*, arteria epigastrica anterior; *A.I.*, arteriæ interdigitales; *A.I.E.*, arteria interossea externa; *A.Io.*, arteria interossea; *A.Pa.*, arteria parietalis; *A.P.B.*, arteria profunda brachii; *A.R.*, arteria radialis; *A.R.R.*, arteria radialis recurrens; *A.S.*, arteria scapularis; *A.S.C.*, arteria subclavia; *A.U.*, arteria ulnaris; *A.U.R.*, arteria ulnaris recurrens; *A.V.*, arteria volaris; *A.V.P.*, arcus volaris profunda; *D.Ao.*, dorsal aorta; *R.E.A.* 1 and 2, rami musculares of arteria epigastrica anterior; *R.P.B.* 1, 2 and 3, rami musculares of arteria profunda brachii; *R.r.*, ramus radialis of arteria volaris; *R.r.* 1, ramus radialis of arcus dorsalis; *R.u.*, ramus ulnaris of arteria volaris; *R.u.* 1, ramus ulnaris of arcus dorsalis; *S.A.*, systemic arch; *Scap.*, scapula; I, hallux; II—V, digits.

gives off twigs to the neighbouring muscles and also a coracoid artery (II. *a*).

B. II. *a. Arteria coracoidea.*—This is distributed to the musculature in the coracoid region.

B. III. *Arteria epigastrica anterior* (A. mammaria externa, Corti) (text-figs. 5 and 6).—The anterior epigastric artery arises in the axillary region, and

after giving off two twigs (B. III. $\alpha$ and $\beta$) passes ventrally along the second rib. It then turns caudally a little to one side of the mid-ventral line, and runs backwards towards the posterior epigastric and the two probably anastomose.

B. III. $\alpha$. *Ramus muscularis* 1.—A small muscular branch of the epigastric runs to the proximal ends of some of the muscles on the posterior side of the brachium.

B. III. $\beta$. *Ramus muscularis* 2.—This is also a small vessel going to the inner sheet of the ventral region of the latissimus dorsi.

The main vessel now becomes the *Arteria brachialis* (text-figs. 5 and 6).

B. IV. *Arteria profunda brachii* (Corti, Zuckerkandl (text-fig. 5)).—The distribution of this artery is fairly typical, the trunk and its branches supply the triceps, supra-coracoideus, coraco-brachialis, and the humeral insertion of the pectoralis, following the nomenclature of Osawa (62). It gives off branches (B. IV. $\alpha$, $\beta$, and $\gamma$) at the proximal end, and another as it passes down (B. IV. $\delta$). Finally, it comes to lie beside the nervus radialis, and may be termed the collateralis radialis (Zuckerkandl). It passes with the radialis nerve through the ectepicondylar foramen.

B. IV. $\alpha$. *Ramus muscularis* 1.—This is a small branch going to the coraco-brachialis muscle.

B. IV. $\beta$. *Arteria circumflexa humeri anterior* (Corti ?).—This vessel passes around the head of the humerus and has approximately the same distribution as the anterior circumflex of Corti, although it arises from the profunda brachii and not from the brachial artery.

B. IV. $\gamma$. *Ramus muscularis* 2.—A small branch runs backwards to the ventral part of the latissimus dorsi muscle.

B. IV. $\delta$. *Ramus muscularis* 3.—A fairly small branch supplies the coraco-brachialis muscle.

B. V. *Arteria bicipitalis* (Zuckerkandl) (Plate 8, fig. 8, text-fig. 5).—A vessel arises about half way to the foramen and mainly serves the biceps.

B. VI. *Arteria collateralis ulnaris* (Corti, Zuckerkandl) (text-fig. 5).—A smallish artery arises from the brachial just above the entepicondylar foramen, and runs close to the ulnaris branch of the nervus medianus. It apparently anastomoses with the recurrent ulnar artery.

The main vessel after passing through the foramen may now be termed the *Arteria interossea* (Plate 8, fig. 9, text-fig. 5).

B. VII. *Arteria radialis* (Corti, Zuckerkandl) (text-fig. 5).—The radial artery arises from the main trunk, shortly after it has passed through the entepicondylar foramen and shortly below this point it gives off a branch (VII. $\alpha$).

The greater part of its course lies in the sulcus radialis, but on nearing the carpus it becomes more superficial.

B. VII. $\alpha$. *Arteria radialis recurrens* (Corti, Zuckerkandl).—This runs backwards and supplies the muscles in the neighbourhood of the elbow.

B. VIII. *Arteria ulnaris* (Corti, Zuckerkandl) (Plate 8, fig. 9, text-fig. 5).—The ulnar artery arises a little beyond and is more deeply situated than the radial, and after giving off a branch (VIII. $\alpha$) runs near the ulnar nerve to the wrist, where it splits into two. The smaller dorsal vessel passes to the dorsal surface of the hand and the ventral forms a fairly typical *Arcus volaris profundis* in conjunction with a branch from the interosseus (*q.v.*).

B. VIII. $\alpha$. *Arteria ulnaris recurrens*.—A twig passes backwards supplying the elbow muscles and anastomosing with the collateralis ulnaris artery (B. VI).

B. IX. *Arteria interossea externa* (Zuckerkandl) (Plate 8, fig. 8, text-fig. 5).—Rather nearer the wrist than the elbow the interosseus artery gives off a short branch, the external interosseus, which divides into proximal and distal branches that lie close to the dorsal branch of the nervus radialis. The descending branch anastomoses with the arcus dorsalis.

B. X. *Arteria volaris* (Plate 8, fig. 9, text-fig. 5).—When the interosseus artery reaches the ends of the radius and ulna it dives down on to the flexor surface of the hand and under the intermedium gives off a short volar artery. This, together with a terminal branch of the ulnar artery, gives rise to the deep volar arch which commences as two vessels, a radial (B. X. $\alpha$) and an ulnar (B. X. $\beta$).

B. X. $\alpha$. *Ramus radialis* (R. medianus, Zuckerkandl).—This passes outwards and sends a twig to the outside of the pollex, and one to split over the space between the first and second digits.

B. X. $\beta$. *Ramus ulnaris* (R. lateralis, Zuckerkandl).—The ulnar branch of the volar arch runs outwards, giving a twig to the outside of the fifth digit and three others. These split over the spaces between digits five and four, four and three, and three and two respectively. From the last of these branches an anastomosis runs to the last branch of the ramus radialis so forming a complete arterial ring in the palm.

The arteria interossea, after giving off the volaris as described above, returns through the carpus just in front of the os intermedium on to the extensor surface of the hand, and here breaks into the two branches (B. XI and XII) which constitute the *Arcus dorsalis*. This peculiar course of the interosseus from the extensor surface down between the ends of the radius and ulna on to the flexor side and then back again through the carpus is evidently primitive, since it is met with in the Amphibia.

B. XI. *Ramus radialis* (ZUCKERKANDL).—The radial branch of the arcus dorsalis receives the anastomosing twig of the external interosseus, and gives off branches to the outside of the pollex and other interdigital twigs to split over the spaces between digits one and two and digits three and four.

B. XII. *Ramus ulnaris* (ZUCKERKANDL).—The ulnar branch of the arcus dorsalis sends a twig to the outside of the fifth digit, and interdigital arteries to the space between five and four and between four and three.

C. *Arteriæ parietales* (text-fig. 6).—From the point of union of the two systemic arteries to form the dorsal aorta, paired parietal arteries come off from this common trunk. Excluding the pair given off from the sub-clavian arteries, seventeen or more usually eighteen pairs can be found before the point of origin of the iliac arteries.

D. *Arteria œsophagea* (HOCHSTETTER).—A small œsophageal artery arises just behind the third parietals.

E. *Arteria gastrica* (HOCHSTETTER) (text-fig. 6).—The gastric artery leaves the dorsal aorta about the level of the fifth pair of parietals and runs to the anterior end of the stomach.

F. *Arteria cœliaca* (HOCHSTETTER; Superior mesenteric, BEDDARD) (text-fig. 6).—The cœliac artery is a large vessel coming from the dorsal aorta near the tenth parietal artery. It is largely concerned with the supply of the stomach and liver, but also serves various other organs by means of a series of branches (F. I–VII), and continues as a large vessel supplying the posterior region of the stomach.

F. I. *Arteria lienalis minor.*—A small artery goes to the spleen.

F. II. *Arteria lienalis major.*—This is the main supply of the spleen.

F. III. *Arteria pancreatica major.*—This is the main vessel going to the pancreas, and shortly after its origin it gives off a small twig to the spleen.

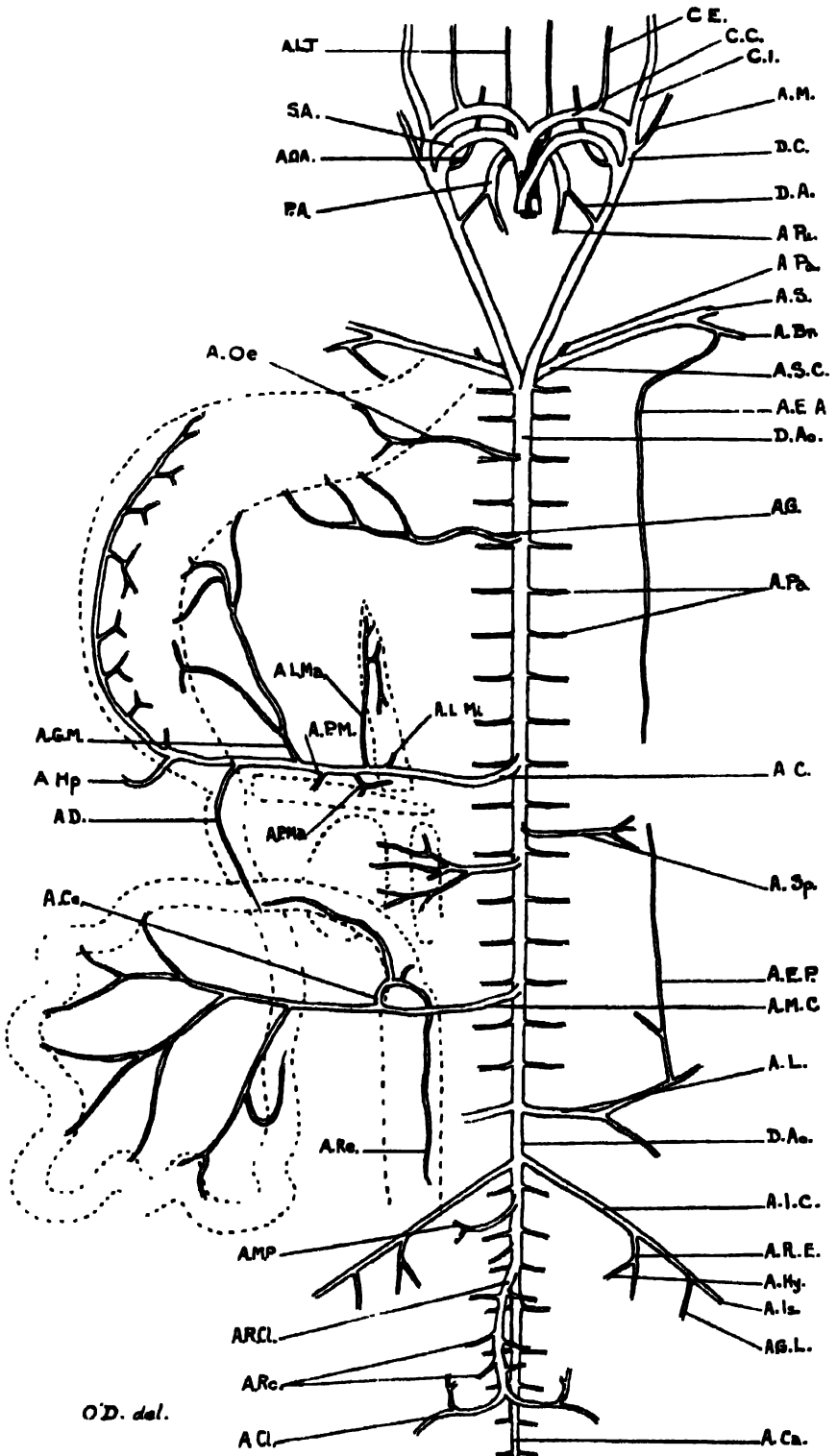
F. IV. *Arteria pancreatica minor.*—A second small twig also goes to the pancreas.

F. V. *Arteria gastrica medialis* (text-fig. 6).—This is a fairly large branch that almost immediately divides into two supplying the mid-region of the stomach. In some specimens the two branches appear to come off separately but close together from the main trunk.

F. VI. *Arteria duodenalis* (A. duodenalis superior, KLAATSCH).—The duodenal artery supplies the proximal part of the intestine.

F. VII. *Arteria hepatica.*—The hepatic artery leaves the main vessel just before it runs on to the stomach wall and enters the liver more or less ventrally.

G. *Arteria spermatica* (text-fig. 6).—This vessel runs to the supra-renal body to which it gives a number of branches, and another set of branches run on to the testis. The left arises a short distance in front of the right. Unfortunately




*A.Br.*, arteria brachialis; *A.C.*, arteria cœliaca; *A.Ca.*, arteria caudalis; *A.Ce.*, arteria cœcalis; *A.Cl.*, arteria cloacalis; *A.D.*, arteria duodenalis; *A.E.A.*, arteria epigastrica arteria; *A.E.P.*, arteria epigastrica posterior; *A.G.*, arteria gastrica; *A.Gl.*, arteria glutea; *A.G.M.*, arteria gastrica media; *A.Hp.*, arteria hepatica; *A.Hy.*, arteria hypogastrica; *A.I.C.*, arteria iliaca communis; *A.I.E.*, arteria iliaca externa; *A.Is.*, arteria ischiadica; *A.L.*, arteria lumbalis; *A.L.Ma.*, arteria lienalis major; *A.L.Mi.*, arteria lienalis minor; *A.L.T.*, arteria laryngeo-trachealis; *A.M.*, arteria muscularis cervicis; *A.M.C.*, arteria mesenterica communis; *A.M.P.*, arteria mesenterica posterior; *A.O.A.*, arteria œsophagea anterior; *A.Oe.*, arteria œsophagea; *A.Pa.*, arteria parietalis; *A.P.Ma.*, arteria pancreatica major; *A.P.Mi.*, arteria pancreatica minor; *A.Pu.*, pulmonary arch; *A.Re.*, arteria recti; *A.R.Cl.*, arteria reno-cloacalis, *A.Re.*, arteria renales, *A.S.*, arteria scapularis, *A.S.C.*, arteria subclavia; *A.Sp.*, arteria spermatica; *C.C.*, carotis communis, *C.E.*, carotis externa; *C.I.*, carotis interna; *D.A.*, ductus arteriosus (BOTALLI); *D.Ao.*, dorsal aorta; *D.C.*, ductus caroticus; *P.A.*, pulmonary arch; *S.A.*, systemic arch.

TEXT-FIG. 6.—Diagram of the Main Arteries of the Body Region in *Sphenodon*, with the alimentary canal pushed out to the right side of the animal. The dotted lines indicate approximately the position of certain of the viscera.

I have not had the opportunity of examining this vessel satisfactorily in the female, but doubtless as the ovary is disposed fairly similarly to the testis with regard to the supra-renal body the distribution of the vessel is much the same.

H. *Arteria mesenterica communis* (Hochstetter) (Plate 6, fig. 1, text-fig. 6).—This vessel arises in the region of the fifteenth pair of segmental arteries, and I find that its distribution agrees more closely with the account given by Hochstetter (44) than with that given by Klaatch (50). The main trunk runs on to the upper part of the intestine and gives off a series of three or four large branches to the intestinal region. Soon after its origin it gives off a large factor (H. I) to the lower end of the intestine.

H. I. *Arteria cæcalis* (Hochstetter).—After giving off a small twig to the junction of the intestine and rectum and a large one to the rectum (H. I. α) this artery runs along the end part of the intestine.

H. I. α. *Arteria recti.*—The rectal artery passes down along the dorsal wall of the rectum and anastomoses with the end of the posterior mesenteric artery.

J. *Arteriæ vasis efferentis.*—There are a series of three small vessels running to the vasa efferentia.

K. *Arteria lumbalis* (Plate 6, fig. 1, text-fig. 6).—The seventeenth or more usually the eighteenth parietal artery is much enlarged and constitutes a lumbar artery. It is distributed to the body wall and gives off two branches (K. I and K. II).

K. I. *Arteria epigastrica posterior.*—This posterior epigastric artery gives off a branch running inwards and forwards to the dorsal body wall and then itself continues on to the ventral body wall, where it turns and runs forwards and appears to anastomose with the anterior epigastric artery.

K. II. *Ramus muscularis.*—The muscular branch runs to the proximal ends of some of the muscles of the posterior surface of the thigh.

L. *Arteria iliaca communis* (Gaupp) (Plate 6, fig. 1, text-fig. 6).—This is a large artery supplying the hind limbs and it arises shortly behind the lumbar artery. It gives off an internal iliac artery (L. I) and then may be termed the external iliac artery. On reaching the limb it gives off a branch to the muscles of the proximal end of the thigh and the pelvic girdle (L. II). It then enters the leg and follows the ischiadic nerve and so may be termed the Arteria ischiadica (*i.e.*, the sciatic artery of many English text-books). Between the head of the femur and the knee it gives off several branches (L. III–VII). Zuckerkandl (84, p. 264) remarks that "Keine der hinteren Unterschenkelarterien kann ungeschwungen mit jenen der Säuger homologisiert werden," and the same is true also of the arteries of the thigh. Although he recognises internal and external circumflex arteries, for example, they both come off from the ischiadic and not from the femoral artery and they have not quite the

same distribution.* The account of these branches down to the knee does not quite agree with that of ZUCKERKANDL, but the difference is slight and only in matters of detail. After passing the knee the main trunk, now termed by ZUCKERKANDL the Arteria interossea, gives off a deep branch to the flexor side (L. VIII), the lateral artery of that author. He also describes a further medial artery (VII. *a*) coming off at this point, but I have been unable to make it out satisfactorily. Almost immediately two arteries come off in succession; the first is a circumflex (IX) and the other a posterior muscular branch (X). The interosseus then runs on to the extensor side of the limb giving off an external interosseus (XI), after which it is bridged by a ligamentum tibio-fibulare, and on to the foot where it may be termed the Arteria dorsalis pedis. This gives off a vessel, the perforans plantaris (XII), which goes through on to the flexor side of the foot and then finally the main trunk breaks up into two terminal branches, an internal (XIII) and an external (XIV).

L. I. *Arteria iliaca interna* (GAUPP).—This artery supplies several of the muscles adjacent to its origin and gives off an important branch (L. I. *a*).

L. I. *a*. *Arteria hypogastrica*.—The hypogastric artery passes ventro-mesially to the wall of the bladder.

The main trunk may here be termed the *Arteria iliaca externa* (Plate 6, fig. 1, text-fig. 6).

L. II. *Arteria glutea* (GAUPP).—The gluteal artery supplies the muscles and tissues of the gluteal region and also a part of the proximal end of the hind limb.

The main trunk here becomes the *Arteria ischiadica* (Plate 8, fig. 4).

L. III. *Arteria circumflexa femoris externa* (ZUCKERKANDL) (Plate 7, fig. 4).—The external circumflex artery is a moderate sized vessel, running to the proximal external muscles of the thigh.

L. IV. *Arteria circumflexa femoris interna* (ZUCKERKANDL) (Plate 8, fig. 4).—The internal circumflex artery is a distinct branch, supplying the adductor and other internal muscles at the top end of the thigh.

L. V. *Ramus muscularis* 1.—This artery runs down on the inner side of the ischio-tibialis muscle, and in some respects recalls the profunda artery, but, unlike it, gives off a circumflex branch (L. V. *a*).

L. V. *a*. *Arteria circumflexa genu interna*.—A small artery passes round and supplies the muscles at the lower external end of the femur.

* The arteria ischiadica is normally replaced by the arteria femoralis as the main vessel of the leg of man, but it may persist and retain its original importance in certain instructive anomalous cases, as recorded by DUBREUIL (24), KRAUSE (51), and RUGE (71).

L. VI. *Ramus muscularis* 2.—Another artery arises from the ischiadic a short distance before the knee and passes to the deeper internal muscles.

L. VII. *Arteria circumflexa genu externa* (Plate 8, fig. 4).—This circumflex artery comes off immediately above the knee and passes round its external side.

The main trunk now becomes the *Arteria interossea* (Plate 8, fig. 4).

L. VIII. *Arteria tibialis lateralis* (Plate 7, figs. 4 and 5).—This is probably the artery described by ZUCKERKANDL (*loc. cit.*) as the lateral artery, for it accompanies the nervus tibialis posticus. It runs down to the plantar surface of the foot, and takes part in the formation of the arcus plantaris, together with a branch from the external tarsal, the tibialis medialis, the perforans plantaris, and the internal tarsal. The plantar arch gives off four branches, the arteriæ interdigitales, that split over the spaces between the digits. The first of the four anastomoses with the external tarsal, and a fifth branch runs to the outside of the hallux and anastomoses with a twig from the internal tarsal. The third and fourth of these arteries are also joined by an anastomosis across the base of the third digit. This showed clearly on one specimen, but not in others, and may be an individual variation. The perforans plantaris (XII) joins the plantar arch on the radial side at the point where the fifth branch, *i.e.*, that to the outside of the hallux, is given off.

L. VIII. *α. Arteria tibialis media* (Plate 8, fig. 5).—ZUCKERKANDL describes a medial branch coming off from the interossea at this point, and running down the tibia, with a large branch of the nervus tibialis, into the depths of the foot. I have not been able to find this vessel. There is, however, a small artery which appears to be a branch of the perforans plantaris, running up the distal end of the tibia with the nervus tibialis medius. This, as will be seen, corresponds with the end of the deep-lying medial artery of ZUCKERKANDL, and so may be the same vessel.

L. IX. *Arteria circumflexa genu interna inferior.*—The inferior circumflex artery of the knee comes off just below the articulation, and supplies the adjacent internal musculature.

L. X. *Ramus muscularis* 3.—A muscular branch runs externally, and probably supplies the peroneus and other adjacent muscles.

L. XI. *Arteria interossea externa* (Ramus dorsalis, ZUCKERKANDL) (Plate 8, fig. 4).—About half way to the ankle, near the interstitium interosseum, an external interosseus artery is given off, which is related to the main interosseus much in the same way as the corresponding vessel of the fore limb. It has two terminal branches, one of which runs up and one down the limb supplying the external muscles.

The main vessel now becomes the *Arteria dorsalis pedis* (Plate 8, fig. 5).

L. XII. *Arteria perforans plantaris* (Plate 8, fig. 5) (Ramus perforans plantaris, ZUCKERKANDL).—The perforans plantaris goes through the ankle between the distal extremities of the tibia and fibula on to the plantar side. Here, as pointed out above, it gives off the tibialis media (L. VIII. *α*, *q.v.*), and joins the arcus plantaris near the base of the hallux.

L. XIII. *Arteria metatarsalis interna* (Plate 8, fig. 4).—The internal tarsal artery soon divides into three branches. One anastomoses with the fifth branch of the plantar arch around the external side of the base of the hallux. The other two are *Arteriæ interdigitales*, splitting over the spaces between digits one and two and two and three respectively.

L. XIV. *Arteria metatarsalis externa* (Plate 8, fig. 4).—The external tarsal artery breaks into two *Arteriæ interdigitales*, which divide over the intervals between digits three and four and four and five. The latter of these gives off a branch, which anastomoses with the first branch of the plantar arch.

M. *Arteria mesenterica posterior* (HOCHSTETTER) (text-fig. 6).—This is a small but distinct artery coming off a little posterior to the ischiadic artery, and distributed to the dorsal wall of the rectum. It gives off a ramus ascendens, which probably anastomoses with the rectal artery (H. I. *α*, *vide supra*).

N. *Arteria reno-cloacalis* (text-fig. 6).—The reno-cloacal artery is a small, well-marked median vessel arising shortly behind the posterior mesenteric and passing between the kidneys, to which it gives branches (N. I). Near the posterior ends of these organs the vessel divides into two branches, the cloacals (N. II).

N. I. *Arteriæ renales.*—The renal arteries consist of about three pairs of vessels, running into the substance of the kidneys.

N. II. *Arteria cloacalis.*—The cloacal artery passes outwards, and is distributed to the lateral wall of the cloaca and extreme end of the rectum. It gives off a branch, which runs to the posterior margin of the cloaca.

After giving off the reno-cloacal artery, the dorsal aorta passes into the hæmal canal of the caudal vertebræ, and so becomes the *Arteria caudalis*. It gives off small paired parietal arteries to the muscles of the tail.

### *The Pulmonary Arch* (text-figs. 1 and 6).

The pulmonary arch, the sixth of the embryonic series and the third of those remaining in the adult, is the most posterior and the most dorsal of the three. It arises well behind the anterior ends of the atria, and runs sharply dorsalwards and backwards, giving off a branch (A) to the larynx, trachea, and œsophagus, and (B) the pulmonary artery itself. From the point of origin of the pulmonary artery, only

a short distance from the heart, the pulmonary arch continues outwards as a narrow, but nevertheless distinct, vessel, the ductus arteriosus or ductus Botalli, which runs into the systemic arch. This vestigeal vessel, whose significance has been pointed out previously (60), is present in an equally developed condition on both sides.

A. *Arteria laryngeo-trachealis* (Laryngeal artery, VAN BEMMELEN) (text-fig. 6).—This interesting vessel arises from the pulmonary arch a short distance from the heart. It was overlooked by RATHKE (66), who examined *Sphenodon*, but it was noted by VAN BEMMELEN (10), who also claims to have found it in *Platydactylus*, *Lacerta*, *Anguis*, *Pseudopus*, and *Iguana*. In company with the laryngeal nerves and the tracheal vein, it passes up the side of the trachea, to which it sends small twigs, finally breaking up in the larynx. It gives off a number of branches (I–VII).

The interest of this vessel lies in the fact that it is undoubtedly homologous with the arteria œsophagea of *Triton*, *Salamandra*, and *Spelerpes* as described by BETHGE (11). In these Urodela the respiration is carried on not only by the skin and lungs, but also by the mucosa of the buccal cavity and pharynx. Indeed, in *Spelerpes*, where the lungs have been completely suppressed, it is performed entirely by the skin and the mucosa in these regions. We find as a result in this form that the pulmonary artery has disappeared, and the only branch of the pulmonary arch that remains is the very large œsophageal artery, which ramifies over the whole of the pharynx, œsophagus, and even the stomach. This relic of what is an important vessel in the Urodele Amphibia persists in certain Lacertilia as noted above, but appears to be best developed in *Sphenodon*.

A. I. *Arteria thyreoidea inferior* (VAN BEMMELEN).—This is a small artery going to the middle loop of the thyroid gland. VAN BEMMELEN (*loc. cit.*) remarks that he found this double arterial supply, partly from the pulmonary and partly from the carotid arches, going to the thyroid gland in all the Saurians he examined, but not in other Reptiles.

A. II–V. *Arteriæ œsophageæ* (Plate 7, fig. 3, text-fig. 7).—A series of small œsophageal branches are given off from the main vessel as it ascends the neck.

A. VI. *Arteria anastomotica* (text-fig. 7).—This is a small artery which anastomoses with its fellow ventrally to the posterior end of the larynx.

A. VII. *Arteria laryngea inferior* (text-fig. 7).—The inferior laryngeal artery breaks up into a number of twigs supplying the larynx and the genio-glossus muscle.

B. *Arteria pulmonalis.*—The pulmonary artery arises from the arch a short way beyond the laryngeo-tracheal artery and runs down the dorso-lateral border of the lung to which it is attached.

## The Venous System.

Considering the work that has been done on the vascular system of the Reptiles in general it is astonishing that there is nothing in the nature of a complete description of the venous system of *Sphenodon*, or of any Lacertilian. Even Corti, who has given such a detailed account of "*Psammosaurus griseus*," dismisses the veins in a couple of pages, remarking that he has neither successfully injected them nor dissected them out. Certain points have been dealt with in a fairly full manner, however.

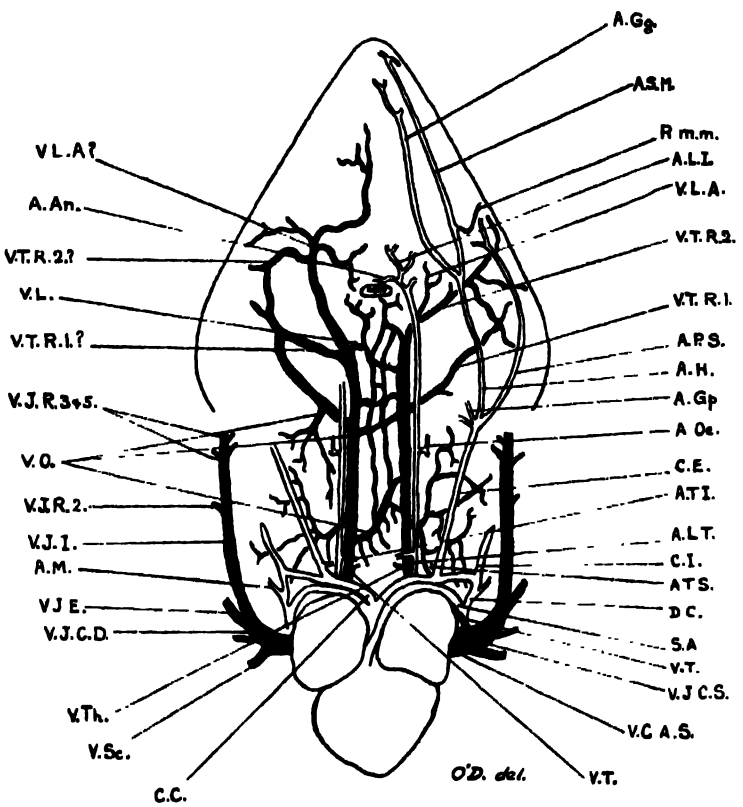
Rathke (65) again provided the starting point of our modern knowledge by his account of the development of *Tropidonotus natrix*. This was added to by the work of Hofmann (47) on the development of the venous system in *Lacerta agilis*. Hochstetter (46) has dealt with the development of the veins in both *Lacerta* and *Tropidonotus*, but confined his attention mainly to the veins posterior to the heart, confirming and extending the observations of Hofmann. The development of the veins in the head and neck, again in *Lacerta* and *Tropidonotus*, have also been well described by Grosser and Brezina (40). Further, we have the interesting work on the cephalic vessels in *Lacerta agilis*, *Tropidonotus natrix*, and *Emys Europæa* by Bruner (18), in which he describes not only the vessels of the adult very fully, but also a muscular mechanism connected with them, whereby the venous blood pressure in the head can be raised. This is apparently called into action during the process of sloughing the skin. In addition to these more or less particular studies, a great number of comparative points have been cleared up in a valuable series of papers by Beddard (2–5, 7 and 8). Lastly, concerning *Sphenodon* itself, we have the work of Dendy (22) on the intra-cranial vessels, including the veins, so that as in the case of the arteries it is only necessary to indicate the relationship of the extra-cranial trunks to them. There is also a description of the sinus venosus in a paper by Röse (70).

As has already been indicated in dealing with the heart, the three main veins of the body, the two anterior and the single posterior venæ cavæ open into a distinct sinus venosus. The two procaval veins are similar in origin, and as the only differences between them are in the relative sizes of their constituent veins, it is only necessary to describe one of them in detail. In dealing with the venous system, the plan is often adopted of commencing with the smallest vessels and working gradually through the larger trunks to the heart. While this has certain advantages and indicates the direction of the blood flow, it is not the general method pursued in actual dissection. The vessels are usually found by following up the larger trunks away from the heart towards the periphery, and that is the plan adopted in the following description.

*Vena cava anterior sinistra* (Plate 7, fig. 3, text-fig. 7).—The left precaval vein is a short stout trunk opening into the dorsal side of the sinus venosus, and formed a

short distance from the heart by the union of three veins, the tracheal (A), the common jugular (B), and the sub-clavian (C).

A. *Vena trachealis* (GROSSER and BREZINA, BRUNER) (text-fig. 7).—The left tracheal vein runs from its point of entry into the left precaval vein, dorsal to the systemic and carotid arches, up the left side of the trachea. It receives tributaries (A. I–X) on its way to the larynx, some of which anastomose with their fellows of the other side and produce a venous network on the ventral side of the œsophagus. In the laryngeal region it receives further branches (XI–XII) from the muscles of the floor of the mouth. The constitution of the right tracheal vein is on the whole similar to that




TEXT-FIG. 7.—Diagram to show the distribution of the Venæ Tracheales and adjacent Arteries. The trachea has been cut off close to the larynx and removed.

*A.An.*, arteria anastomotica; *A.Gg.*, arteria genioglossa; *A.Gp.*, arteria glossopharyngeus; *A.H.*, arteria hyomandibularis; *A.L.I.*, arteria laryngea inferior; *A.L.T.*, arteria laryngeo-trachialis; *A.M.*, arteria muscularis cervicis; *A.Oe.*, arteria œsophagea; *A.P.S.*, arteria pterygoideus superficialis; *A.S.M.*, arteria sub-mandibularis; *A.T.I.*, arteria thyreoidea inferior; *A.T.S.*, arteria thyreoidea superior; *C.C.*, carotis communis; *C.E.*, carotis externa; *C.I.*, carotis interna; *D.C.*, ductus caroticus; *R.m.m.*, ramus musculo-mandibularis; *S.A.*, systemic arch; *V.C.A.S.*, vena cava anterior sinistra; *V.J.C.D.*, vena jugularis communis dextra; *V.J.C.S.*, vena jugularis communis sinistra; *V.J.E.*, vena jugularis externa; *V.J.I.*, vena jugularis interna; *V.J.R.I.*, rami musculares of v. jugularis interna; *V.L.*, vena laryngea; *V.L.A.*, vena laryngea anterior; *V.O.*, venæ œsophageæ; *V.Sc.*, vena subclavia; *V.T.*, vena trachealis; *V.Th.*, vena thyreoidea; *V.T.R.* 1 and 2, rami musculares of v. trachealis.

of the left, but the former is considerably larger and has more branches. In the embryo of *Lacerta*, according to both BRUNER (18) and GROSSER and BREZINA (40), a tracheal vein is present on both sides. During the course of development, however, anastomoses arise between them, no doubt corresponding to those in the adult *Sphenodon*, which allow of the complete disappearance of the posterior portion of the left vein in later stages. Thus it follows that in the adult only the right tracheal vein persists, as pointed out by PARKER (64), who, however, calls it quite wrongly (p. 161) the external jugular vein, and by VOGT and JUNG (78), who term it "die unpaare Kopfvene" (p. 714).

The condition in *Sphenodon* is noteworthy, since it is more primitive than that in *Lacerta*, and, moreover, represents a stage passed through by the latter animal in the course of its development. Further, the left vein in *Sphenodon* is much smaller than the right, as if foreshadowing its partial disappearance in other forms.

The vena trachealis in *Sphenodon* and *Lacerta* is an interesting vein, for, as will be seen from the above account, its distribution is very similar to that of the external jugular of the Amphibia, but at the same time it is obviously not the same vessel. In the frog, as is generally known, and in *Salamandra*, *Triton*, and *Spelerpes*, according to BETHGE (11), the external jugular is a fairly superficial vein running *ventrad* of the arterial arches and receiving two main tributaries, the vena lingualis and vena mandibularis. The tracheal vein in *Sphenodon* passes *dorsad* of the arterial arches and does not receive two such definite vessels, although it drains very nearly the same territory. There is present in the three Urodeles a vessel from which it seems easily possible to derive the vena trachealis of the Saurians, and that is the vena pharyngea (BETHGE). This vessel arises posterior to the arterial arches and its course lies dorsal to them along the wall of the pharynx. It will easily be seen then that anastomoses between it and the lingualis would enable it to take over the latter and through it the mandibularis, thus reducing the vena jugularis externa in *Sphenodon* (*q.v.*) to the unimportant vessel that it is.

A. I. *Vena thyreoidea* (text-fig. 7).—The thyroid gland is drained by a small vein entering the tracheal vein near its proximal end.

A. II–V. *Venæ œsophageæ* (text-fig. 7).—A number of veins come from the walls of the œsophagus. Some come inwards from the lateral wall and others outwards from the ventral wall. The latter take part in the formation of the venous network already described.

A. VI. *Ramus muscularis* 1.—This is a vein coming from the inner surface of the internal pterygoid muscle.

A. VII–X. *Venæ laryngeæ*.—The laryngeal veins are a series of small branches coming from the posterior muscles of the larynx. They anastomose with

similar vessels from the right, and also have twigs from the anterior end of the œsophagus running into them.

A. XI. *Ramus muscularis* 2.—This is a fair-sized vein, running outwards from the side of the larynx and receiving three tributaries :—

XI. $\alpha$. A branch that anastomoses with A. VI.

XI. $\beta$. A branch coming backwards from the lateral surface of the internal pterygoid muscle.

XI. $\gamma$. A branch coming forward from the same surface of the internal pterygoid muscle.

A. XII. *Vena laryngea anterior* (text-fig. 7).—The anterior laryngeal vein bends round the lateral wall of the larynx and receives three main branches :—

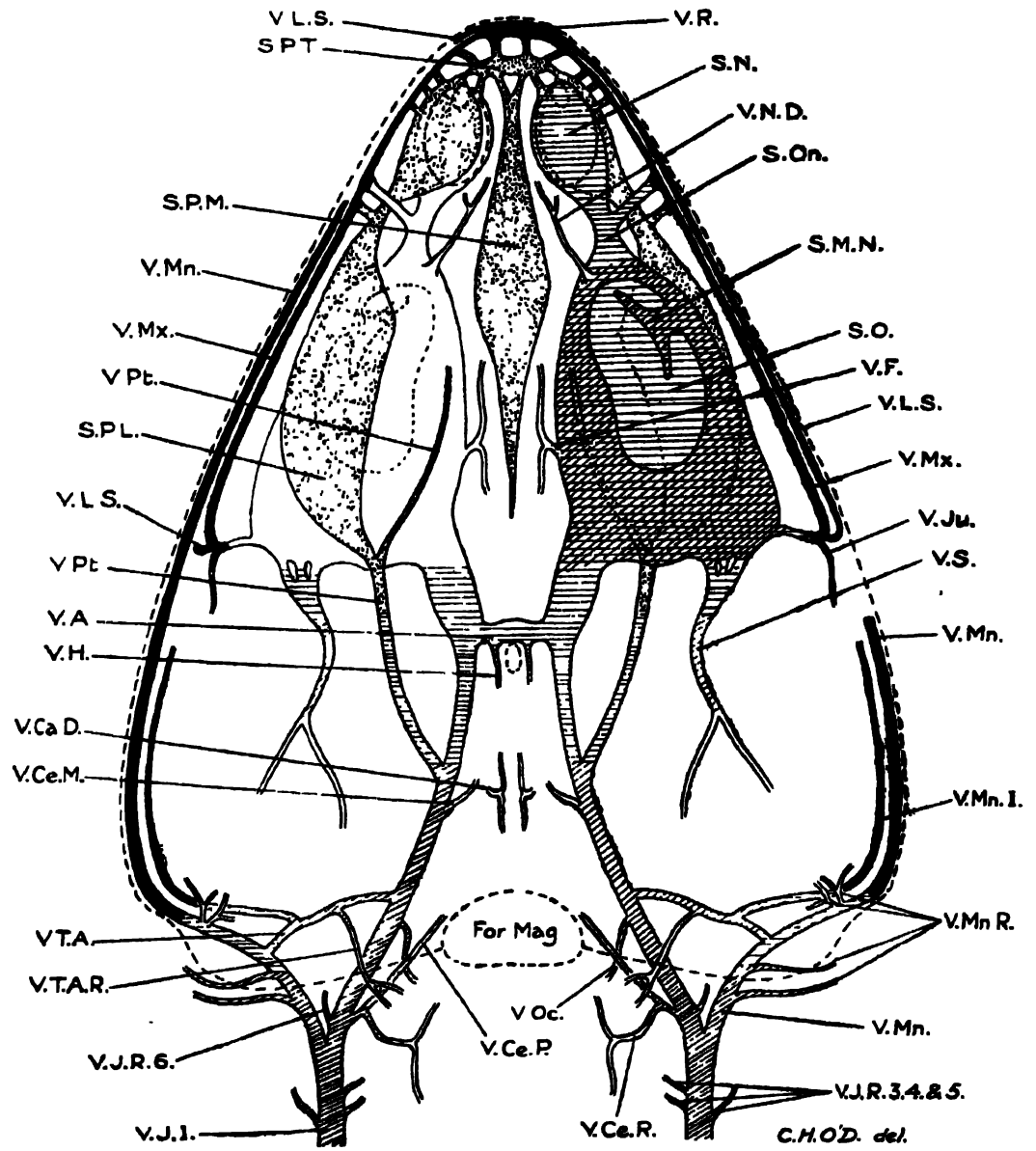
A. XII. $\alpha$. A branch from the lateral and anterior walls of the larynx.

A. XII. $\beta$. A branch from the cerato-mandibular muscle.

A. XII. $\gamma$. A branch from the genio-glossus muscle.

B. *Vena jugularis communis sinistra* (V. jugularis, Corti) (Plate 7, fig. 3, text-fig. 7).—The left common jugular vein is the second of the three trunks that unite to form the left precaval. From its origin it passes slightly laterally and then up the neck, receiving after a short distance a muscularis branch (B. I) and, a little more anteriorly, the external jugular (B. II). From this point it is continued forward as the *Vena jugularis interna* (V. jugularis, Grosser and Brezina ; V. jugularis interna, Bruner), receiving a number of branches (B. III–VI) up to the hinder end of the neck, where it is crossed dorsally by the tenth cranial nerve and the internal carotid artery. Just at this point it receives the large mandibular vein (B. VII). A very short distance in front of this it receives a branch (B. VIII) on its outer side, and on the inner side, at the same level or just anterior to it, the posterior cerebral vein (B. IX). This is an important landmark, as the combined vessel formed by the main trunk up to this point and then continued on as the posterior cerebral vein is homologous with the internal jugular vein of the mammals, including man.

The constitution of the anterior end of the main trunk can only be properly understood in the light of its development. A marked difference between the venous supply in the head of the human embryo and of the adult was first pointed out by Luschka (53), who, however, was not in possession of sufficient data to give a satisfactory explanation thereof. This line of enquiry was carried further by Salzer (72), who worked out the partial replacement of the old "anterior cardinal vein" (*sic*, really vena capitis medialis) in the head region by a more laterally situated trunk, which he termed the vena capitis lateralis. A further paper by




TEXT-FIG. 8.—Diagram of the Venous System of the Head. Vessels in jaws indicated in black. Palatine vessels dotted shading. Vessels at level of ventral side of cranium horizontal shading. Vessels at higher level oblique shading, and most dorsal vessels in outline only. On right side the mandibular vein is cut off short behind level of maxillary vein. The orbital and orbito-nasal veins are fully displayed. On left side the superior labial vein is cut off short at its origin, and the palatine sinuses fully shaded, while the orbital and orbito-nasal sinuses are indicated in outline or dotted outline only.

*For.Mag.*, foramen magnum; *S.M.N.*, sinus membranæ nictitantis; *S.N.*, sinus nasalis; *S.O.*, sinus orbitalis; *S.On.*, sinus orbito-nasalis; *S.P.L.*, sinus palatinus lateralis; *S.P.M.*, sinus palatinus medius; *S.P.T.*, sinus palatinus transversus; *V.A.*, vena anastomotica; *V.Ca.D.*, vena capitis dorsalis; *V.Ce.M.*, vena cerebralis media; *V.Ce.P.*, vena cerebralis posterior; *V.Ce.R.*, ramus muscularis of vena cerebralis posterior; *V.F.*, vena frontalis; *V.H.*, vena hypophyseos lateralis; *V.J.I.*, vena jugularis interna; *V.J.R.* 3, 4 and 5, rami musculares of vena jugularis interna; *V.J.R.* 6, ramus muscularis of vena jugularis interna; *V.Ju.*, vena jugalis; *V.L.S.*, vena labialis superior; *V.Mn.*, vena mandibularis; *V.Mn.I.*, vena mandibularis interna; *V.Mn.R.*, rami musculares of vena mandibularis; *V.Mx.*, vena maxillaris; *V.N.D.*, vena nasalis dorsalis; *V.Oc.*, vena occipitalis; *V.Pt.*, vena pterygoidea; *V.R.*, vena rostralis; *V.S.*, vena supratemporalis; *V.T.A.*, vena tympanica anterior; *V.T.A.R.*, ramus muscularis of vena tympanica anterior.

GROSSER and BREZINA (40) gave an excellent description of the development of the vascular system of *Lacerta* and *Tropidonotus*, and lastly GROSSER (39) reviewed these changes in the vertebrate series. As far as these results apply to Reptilia and particularly Lacertilia, they may be briefly epitomised as follows:—In the fairly early embryo there are present two longitudinal veins in the head and neck. The first is the anterior cardinal vein, probably to be regarded as intimately related to the somites, and starting at their anterior end behind the auditory vesicle. It runs backwards into the Ductus Cuvieri. The second, the vena capitis medialis (GROSSER and BREZINA), lies on the base of the brain ventral to and slightly mesial to the primordia of the cranial nerves, and receives the orbital sinus. These two are connected by means of a more or less transverse vessel, the vena cerebralis posterior (GROSSER and BREZINA), shortly behind the primordium of the tenth cranial nerve. As development proceeds a series of vascular rings are laid down around the primordia of cranial nerves five to ten. The linking up of the outer portions of these rings constitutes another longitudinal venus trunk, the vena capitis lateralis (SALZER), which lies dorsal and slightly lateral to the nerve roots. The vena cerebralis posterior grows upwards and joins with its fellow to help to form the vena longitudinis cerebri, which also acquires two further connections, with the vena capitis medialis and later with the vena capitis lateralis. The hinder of these two connections, the vena cerebralis media (GROSSER and BREZINA), runs round behind the cerebellum and into the vena capitis medialis close by the ganglion of the trigeminus. The front vessel, the vena cerebralis anterior (GROSSER and BREZINA), begins at the epiphysis cerebri and passes behind the cerebral hemisphere into the vena capitis medialis just behind the orbit.

With the subsequent disappearance of the inner longitudinal vessel, the vena capitis medialis, and of the transverse portions of the venous rings, the definitive head vessel comes to consist of three parts. 1. The posterior part, derived from the old anterior cardinal vein, extends up to the vena cerebralis posterior. 2. The median portion from this point on to just in front of the ganglion of the trigeminus is derived from the vena capitis lateralis. 3. The remaining anterior part is the remnant of the vena capitis medialis and the orbital sinus.

The vessel so far described in the adult *Sphenodon* is the posterior part, *i.e.*, the persistent anterior cardinal. The *vena capitis lateralis* portion passes upwards and inwards to the posterior end of the skull, running under the paroccipital bone, dorsal to the columellar auris and dorso-mesial of the bifurcation of the stapedial artery, to form the temporal and mandibular arteries. Just behind the columella auris the occipital vein (B. X) enters the vena capitis lateralis, and in front of the columella it receives the anterior tympanic (B. VII. $\gamma$), which puts it in communication with the mandibular vein. It continues forwards under the paroccipital bone along the ventro-lateral wall of the auditory capsule, on which

its position is faintly marked by a shallow inconspicuous groove, through the foramen between the quadrate wing of the pterygoid bone and the otic capsule (*i.e.*, the foramen for the hyomaxillary branch of the seventh cranial nerve, and termed by WATSON (79) in *Diademodon* the pterygo-paroccipital fossa). Passing dorsal to the roots of the facialis nerve it receives on its dorsal side the median cerebral vein (B. XI) just behind the splitting of the trigeminus, and this marks the end of the vena capitis lateralis portion.

The main trunk, now in its anterior or *vena capitis medialis* portion, runs on ventral of the roots of the trigeminus forwards near the mid-ventral line towards the orbital sinus. A short distance beyond the nerve the pterygoid vein (B. XII) enters the vena capitis medialis, and at the level of the front end of the hypophysis cerebri it receives an anastomosing vein (B. XIII) which puts it into communication with its fellow of the opposite side. Anterior to this the character of the vessel changes, and, from being a vessel with a definite wall, it becomes sinusoidal in nature. The actual vessel can be traced forwards for some distance on the dorso-mesial aspect of the musculus protrusor oculi, as figured by BRUNER (18) in *Lacerta*, but the orbital sinus extends postero-lateral of this and somewhat obscures the vessel. The sinuses ultimately merge into one large *Orbital sinus*, which, although a continuation of the main trunk, can be more conveniently dealt with separately. For the whole of this main venous trunk BRUNER (*loc. cit.*) employs the term vena jugularis interna, but, as pointed out above, only part of it is homologous with the similarly named trunk in the mammals, and, in front of that, we have to deal with at least two portions that are distinct developmentally.

B. I. *Ramus muscularis* 1.—This is a small vessel joining the common jugular close to the heart and coming from the adjacent dorso-lateral muscles. It is not present on the right side of one specimen with the venous system injected, and so may not be constant.

B. II. *Vena jugularis externa* (BRUNER) (Plate 6, fig. 1; Plate 7, fig. 3, text-fig. 7).—There is a well marked vessel joining the internal jugular low down in the neck to form the common jugular vein. This vessel, from its general disposition, is apparently the external jugular vein, but this cannot be regarded as definitely established without reference to its development, for, as has been pointed out previously, it has apparently yielded its lingual and mandibular branches to the tracheal vein (*q.v.*). I have not been able to ascertain whether it is connected with the external mandibular, as BRUNER (18) states the corresponding vessel is in *Lacerta*. This is not improbable, however, since it runs right up the neck ventro-laterad of the cervical nerves as far as the posterior region of the head, draining the superficial muscles and subcutaneous tissue.

The diminution in the functional importance of the external jugular vein in *Sphenedon* and *Lacerta* is interesting, since that vessel is of fair importance in the Amphibia, and is still more important in the Mammalia, where, if it is the same vessel, as seems probable, the external jugular drains the whole of the head and face, leaving practically only the brain to the internal jugular. In spite of the works of SALZER (72), and MALL (55), and SMITH (74), the question of the development of the external jugular vein in the Mammal does not appear to have been satisfactorily worked out. It is not merely that the external jugular in this order retains the factors that it has in the Amphibia, but it also adds to them in some way or other all the territory drained by the capitis lateralis and capitis medialis portions of the main head vein in such a form as *Sphenodon*.

As will be seen from the above accounts, the names Internal and External jugular vein have a very different significance in the different groups of Vertebrates, and the terms should not be employed unless carefully defined.

From this point the main trunk is the anterior cardinal portion of the vena jugularis interna.

B. III. *Ramus muscularis* 2 (Plate 7, fig. 3, text-fig. 7).—This is a vein coming from the cucullaris muscle. It receives a well marked factor, which comes in from the surrounding subcutaneous tissue and penetrates the muscle.

B. IV. *Ramus muscularis* 3.—This is a second twig, draining the anterior part of the cucullaris muscle.

B. V. *Ramus muscularis* 4.—A small vessel returns blood from the longissimus dorsi muscle, and probably also from the deeper layers of the cucullaris.

B. VI. *Ramus muscularis* 5 (Plate 7, fig. 3, text-fig. 7).—Another fairly small vessel comes from the antero-dorsal region of the cucullaris muscle.

B. VII. *Vena mandibularis* (V. maxillaris inferior, GROSSER and BREZINA; V. mandibularis, BRUNER) (text-fig. 8).—The mandibular vein is a well marked tributary, which joins the internal jugular at the point where the latter is crossed by the vagus. It is undoubtedly the same vessel as that described and figured by GROSSER and BREZINA (40), who, however, term it the inferior maxillary, a somewhat misleading name, since it has nothing to do with the maxilla. It passes outwards internal to the anterior cornu of the hyoid and posterior to the mandible, receiving two branches (B. VII. $\alpha$ and $\beta$). Just internal to the quadrato-jugal bone, an important tributary, the anterior tympanic vein (B. VII. $\gamma$) joins it, and, shortly after this, two twigs (B. VII. $\delta$ and $\epsilon$) from the masetter muscle. The main trunk then takes its course along the outer surface of the mandible, finally entering the substance of the bone through a small foramen situated at the end of a short shallow groove. Just before so doing it receives a small external branch.

At this point it seems advisable to call attention to the interesting work of BRUNER (18), who has described a neuro-muscular apparatus connected with the bases of the vena mandibularis and the vena cerebralis posterior and the neighbouring part of the main trunk of the vena jugularis interna in various Lacertilia, Testudinata and Ophidia. It takes the form of a well-developed external muscular sheath, "the musculus constrictor venæ jugularis internæ," enervated by a special nerve supply, whereby the three vessels can be considerably constricted, and the venous pressure in the head greatly increased. The apparatus is useful, apparently, in helping in the operation of shedding the skin. The muscles are fairly easily seen in *Lacerta* and *Tropidonotus*, but are not quite so obvious in *Sphenodon;* they can be made very plain, however, in the following way. If the anterior region of the internal jugular, with a good piece of the ends of both mandibular and posterior cerebral veins, be dissected out, and any coagulated blood in them washed out and the preparation placed in a glass dish of alcohol containing a little glycerine, the muscles can readily be made out. When viewed by transmitted light, the ordinary parts of the vein wall appear moderately transparent and thin-walled, but, in the region occupied by the muscle, the walls of the vessels are very much thicker and more opaque. Transverse sections through the various regions also bring out quite clearly the fact that the bases of both mandibular and posterior cerebral vein, and of the internal jugular in the vicinity, are enveloped by a conspicuous coat of striate muscle, just as BRUNER described in other Saurians. The condition of the specimens did not allow of detailed examination of its nerve supply, but, as it lies quite close to the ganglion glossopharyngei, as in *Lacerta*, the nerves to the muscle, nervi tumefactores capitis, are doubtless fairly similar. For the same reason, the connection of the muscle with the skeleton, if present, could not be satisfactorily ascertained.

I also find myself in agreement with BRUNER with regard to the late appearance of these muscles during the course of development, for they are but feebly shown in the oldest stage I have examined (Stage S of DENDY).

B. VII. $\alpha$ and $\beta$. *Rami musculares* a and b.—These are two small muscular branches entering the mandibular vein in the region of the angle of the jaw from which they come.

B. VII. $\gamma$. *Vena tympanica anterior* (BRUNER) (Plate 7, fig. 2, text-fig. 8).—The anterior tympanic vein is an important tributary joining the mandibular a little further along its course. It passes mesially through the ear cavity anterior to the columella but behind the quadrate to enter the vena capitis lateralis just anterior to the point where it is crossed by the stapedial artery. Thus it forms an anastomosis between the mandibular and lateral head veins. In the region of the mandible it receives the internal mandibular (VII. $\gamma$. i), and dorso-mesiad of this a ventrally running branch (VII. $\gamma$. ii).

VII. $\gamma$. i. *Vena mandibularis interna* (BRUNER) (Plate 7, fig. 2, text-fig. 8).—The internal mandibular vein after leaving the anterior tympanic runs outwards below the quadrate bone and forward along the inner surface of the mandible, which it drains.

VII. $\gamma$. ii. *Ramus muscularis*.—This is a fair sized vessel bringing back blood from the anterior end of the longissimus muscle and the tissues in the region of the post temporal fossa.

B. VII. $\delta$ and $\epsilon$. *Rami musculares* c and d.—These are two veins which almost immediately re-divide and drain the main mass of the temporo-masetter muscle.

B. VIII. *Ramus muscularis* 6.—This is a short branch from the parieto-mandibularis muscle.

B. IX. *Vena cerebralis posterior* (GROSSER and BREZINA; V. cephalica posterior, VERSLUYS and DENDY) (Plate 2, fig. 2, text-fig. 8).—The posterior cerebral is a small but important vein which passes upwards and inwards from the internal jugular under the cucullaris muscle from which it receives a branch (B. IX. $\alpha$). It takes up a position near the root of the tenth cranial nerve, and with it enters the skull through the jugular foramen. The distribution of this vein and its relations to other vessels within the cranium, where it receives a large posterior factor, the vena spinalis, has been dealt with fully by DENDY (22).

This last author proposes to call this vessel the *vena cephalica posterior*, following VERSLUYS (77), on the grounds that cerebralis is undesirable, as it has "nothing to do with the cerebrum proper" (*loc. cit.*, p. 413). I think on the whole it is better to retain the original terminology of GROSSER and BREZINA for several reasons. As a matter of fact, the adjective cerebral is usually employed in comparative anatomy to indicate a structure related to the brain as a whole, *e.g.*, cerebral carotid, while the term cephalic is used for a vessel related to the head. Thus, to extend the same nomenclature to the second of the transverse brain vessels, the *vena cerebralis media* of GROSSER and BREZINA, would lead to confusion, for median cephalic vein is a much closer translation of the *vena capitis medialis* of these authors, which is a totally distinct vessel. In the second place, VERSLUYS used the term *vena cephalica posterior* in error, probably misreading the lettering in the figures of the original authors, for he says (*loc. cit.*, p. 349): "Die andere kommt durch das Foramen magnum, dann zwischen Schädel und Atlasbogen hindurch aus der Schädelhöhle; GROSSER u. BREZINA haben sie 'Vena cephalica posterior' genannt." These investigators, however, nowhere use the term cephalica, but call the vessel in question the v. cerebralis posterior. Lastly, several subsequent writers, including GROSSER himself, in a comparative account of the head veins of Vertebrates (39), have employed the term cerebralis, which is now fairly widely accepted.

A rather striking difference is to be noted between the situation of the vena cerebralis posterior in *Sphenodon* and in *Lacerta* and *Tropidonotus*. In *Sphenodon*, as has been pointed out, the vein in question leaves the cranial cavity through the jugular foramen, and is in consequence homologous with the so-called internal jugular of mammals and birds. Both VERSLUYS (77) and GISI (34) state that they have been unable to find the posterior cerebral vein in *Sphenodon*, although the former points out that the canal leading from the foramen jugular is wider than would be necessary for the nerve alone. SCHAUINSLAND (73), however, has described the presence of a vein passing through the skull by the jugular foramen in company with the tenth and eleventh cranial nerves. As pointed out by DENDY (22), whose statement I am able to confirm, there is no doubt that the posterior cerebral vein leaves the skull through the foramen jugulare.

VERSLUYS (77), GROSSER and BREZINA (40), and BRUNER (18) are all in agreement that the posterior cerebral vein in *Lacerta* and *Tropidonotus* leaves the cranial cavity by the foramen magnum and not through the foramen jugulare. CLASON (20A) describes in *Lacerta* a fine vein passing through the jugular foramen, but this appears to be either an error in observation or the lizard in question was slightly abnormal, for, as will be seen later, this is also a possible explanation. HASSE (43) in *Tropidonotus* describes a vessel coming out through the foramen jugulare, but this has not been found by subsequent workers, *e.g.*, GROSSER and BREZINA (*loc. cit.*), BRUNER (*loc. cit.*), and O'DONOGHUE (58). It is stated that in all the Lacertilia dissected by VERSLUYS (*loc. cit.*), the vena cerebralis posterior came out by the foramen magnum with the single exception of *Amphisbæna fuliginosa*, in which there was also present a vein issuing from the jugular foramen. The two veins in this species enter the vena jugularis interna. This condition is an interesting one, for it is also realised in *Emys Europæa* (BRUNER), and as GROSSER and BREZINA point out is to be found in *Lacerta* embryo with a head length of 4·1 mm. A similar arrangement is probably to be found in the Crocodile, since RATHKE (68) mentions a vein leaving the cranial cavity in company with the tenth nerve, and another through the foramen magnum. His description is not at all easy to follow, however, and I agree with DENDY that the point must await further investigation. This loop on the posterior cerebral vein shows how it is possible for the two different conditions met with in *Sphenodon* and the Lacertilia to be arrived at, for it simply becomes a question of which part of the loop persists in the adult.

In Elasmobranchs the posterior cerebral vein leaves the skull with the tenth cranial nerve, as was pointed out in the embryo by GROSSER (39) and in the adult by O'DONOGHUE (59). The same happens in both Urodele and Anurous Amphibia according to REX (69), although there is some variation in the relative sizes of the venæ cerebrales posterior and media in this class. Furthermore, we find the vein leaving the skull with the tenth nerve in the Chelonia, according to HASSE (43), and as noted above also in Mammalia and Aves. There can be little doubt, then, that the

condition in *Sphenodon* in this respect is more primitive than in the Lacertilia and Ophidia, and that it approximates more closely to the Urodele Amphibia.

Thus, although a vein of moderate calibre, the vena cerebralis posterior is of considerable morphological importance, since it is one of the most constant veins in the head of Vertebrata and serves as a valuable landmark.

B. IX. *α. Ramus muscularis.*—On its way beneath the cucullaris muscle, the posterior cerebral vein receives a branch from that muscle. It is formed by the union of an interior and posterior factors.

The main vessel now enters on its *Vena capitis lateralis* portion (Plate 7, fig. 2).

B. X. *Vena occipitalis* (Pate 7, fig. 2, text-fig. 8).—The occipital vein runs inwards and downwards from the lateral head vein, which it joins just behind the columella. It returns the blood from the muscles and tissues in the occipital region.

A short distance in front of this the main trunk receives the vena tympanica anterior, B. VII. *γ*, linking it up with the mandibular vein.

B. XI. *Vena cerebralis media* (Grosser and Brezina; Sinus transversus, Dendy) (Plate 7, fig. 2, text-fig. 8).—The intercranial course of this vessel has been dealt with by Dendy, who also describes its passage through the membranous cranial wall and downwards behind the epipterygoid bone into the end of the vena capitis lateralis just by the ganglionated root of the trigeminus. Intra-cranially it enlarges to form a big triangular sinus, and receives a branch, the vena capitis dorsalis (XI. *α*). Bruner (18) describes in the adult *Lacerta* a secondary extra-cranial connection between the median cerebral vein and the orbital sinus. I have not been able to discover any such vein in *Sphenodon.*

Although part of the median cerebral vein is extra-cranial in *Sphenodon*, it lies in close apposition to the membranous cranial wall down to the root of the trigeminus. There seems to be little doubt that it is completely homologous with the vein leaving the cranial cavity with the fifth nerve in such a form as *Ornithorhynchus*, in which the disappearance of the lateral membrane and the formation of a more external bony cranial wall has caused it to become completely intra-cranial. It appears to be a fairly widespread vein, as it occurs generally in the Amphibia, where it sometimes forms the main vessel leaving the cranium, and also in early Reptilia. In *Diademodon*, for example, it probably left the skull through the foramen described by Watson (79, p. 303) for the posterior two roots of the fifth nerve lying at the front end of the groove leading forward from the pterygo-paroccipital foramen.

B. XI. *α. Vena capitis dorsalis* (Bruner; Dendy) (text-fig. 8).—The dorsal head vein drains the muscles in the spino-occipital region, and just before

piercing the skull to enter the median cerebral vein it receives an anterior factor from above the parietal bone, the *vena parietalis* of BRUNER. Apparently it passes through the skull by a small foramen in the parietal bone or between it and the pro-otic or supra-occipital regions. The exact position of this cannot be made out with certainty in an old skull. It enters the sinus transversus near its origin from the sinus (vena) longitudinalis. Mr. WATSON informs me that the entrance of a vena capitis dorsalis through a foramen or notch in the side of the hinder end of the brain case, either in the pro-otic or supra-occipital, appears to be a constant feature in early Amphibia and Reptilia, and the foramen is figured by him in Diademodon (79, p. 301). This is also noted by ANDREWS (1, p. 87) in Stenosaurus.

The main trunk now enters on its *Vena capitis medialis* portion.

B. XII. *Vena pterygoidea* (BRUNER) (Plate 7, fig. 2, text-fig. 8).—The pterygoid vein joins the lateral cephalic just in front of the trigeminus and the epipterygoid bone. It runs forwards and outwards in company with the palatine branch of the facial nerve and the palatine artery to the region of the sub-orbital foramen, through which it receives a large branch (XII. $\alpha$). The main vessel continues on, passing towards the middle line again, and drains the dorsal surface of the palatine bone. The details of the finer connections at the anterior end cannot be made out satisfactorily by dissection, but are visible in a series of transverse and longitudinal sections of late embryos that Prof. DENDY kindly placed at my disposal.

B. XII. $\alpha$. *Sinus palatinus lateralis* (BRUNER) (text-fig. 8).—The lateral palatine sinus enters the pterygoid vein near the sub-orbital foramen, through which it passes on to the ventral side of the palatine bone. At first a single trunk, it soon forms a sinusoidal network in the sub-mucosa of the palate, passing forward mesiad of the inner tooth row. Beneath the front end of the orbit it again runs together to form a single trunk, only to swell out shortly afterwards to form a large sinus beneath the nasal capsule. In this part of its course it anastomoses with the maxillary vein. Finally, right at the front end of the pre-maxillary region we find it takes its origin in a transverse sinus (XII. $\alpha$ (i)).

XII. $\alpha$ (i). *Sinus palatinus transversus* (BRUNER).—The transverse palatine sinus is a small vessel joining the two lateral palatine sinuses across the middle line, but it is important because of its connections. Laterally it runs into the maxillary vein, and through it is put into communication with a still more anterior transverse trunk, the rostral vein (B. XX). In the middle line the transverse palatine sinus receives the two openings of the median palatine sinus ($\alpha$ (i) a).

$\alpha$ (i) a. *Sinus palatinus medius* (BRUNER).—The median palatine sinus opens by two veins, which soon unite to form a single vessel. This passes back in the middle line and in the mid-orbital region forms a network of veins. Small vessels connect it with the lateral palatine sinus here and there.

B. XIII. *Vena anastomotica* (text-fig. 8).—This anastomosing vein joins the two median cephalic veins as they run along the membranous wall of the cranium just in front of the pre-sphenoid and in front of the hypophysis cerebri. It is a short vessel receiving on each side a branch—the lateral hypophyseal vein (B. XIII. $\alpha$).

B. XIII. $\alpha$. *Vena hypophyseos lateralis* (text-fig. 8).—This vein is here called lateral to distinguish it from the vena hypophyseos of BRUNER, which according to that author is connected with the median cerebral vein. It passes backwards inside the membranous wall of the hypophyseal cavity and apparently joins its fellow just behind the pituitary body. DENDY (22) was not able to find any vessel corresponding to the hypophyseal of BRUNER in the adult, nor does it appear to be present in the embryo.

*Sinus orbitalis* (BRUNER) (Plate 7, fig. 2, text-fig. 8).—Almost immediately in front of the anastomosis, the median cephalic vein becomes enlarged and sinus-like and so constitutes the orbital sinus. The foundation of our knowledge of this region in the Reptilia was laid by WEBER (80), although he took no notice of the veins leading into it. The exact limits of the sinus and point of entry of its tributaries are difficult to make out by dissection, but I have been much aided by the series of sections already mentioned. It is a very large vessel, extending from just in front of the anterior end of the hypophysis, where its hinder limits are marked by the fascia separating it from the temporal fossa, forward to the orbito-nasal septum. Through the fissura orbito-nasalis of GAUPP (32) it communicates with the nasal sinus (B. XIX. $\alpha$). Its floor is formed by the smooth orbital muscle similar to that described by LEYDIG (52) in Lacertilia, and its internal boundary is the septum interorbitale. The sinus therefore occupies practically the whole of the orbit not taken up by the eyeball and its muscles, but it is incomplete dorsally save at the posterior end. Antero-mesially, although it passes up the septum, it only runs for a very short way along the roof of the orbit, and the same occurs antero-laterally, so that the sinus is much smaller at the front than at the back end of the orbit. Although it does not lie above the eyeball at the anterior end, it is in communication there with a subsidiary sinus in the nictitating membrane (B. XVIII). The main sinus by means of a series of tributaries (B. XV–XX) drains almost the whole of the anterior region of the head with the exception of the palate, and it also receives a posterior trunk from the supra-temporal region (B. XIV).

B. XIV. *Vena supra-temporalis* (Bruner) (Plate 7, fig. 2, text-fig. 8).—The supra-temporal vein enters the postero-dorsal border of the orbital sinus slightly anterior to the anastomosing vein. It runs backwards first as a single stem, but afterwards divides into two in the tissue above the temporalis muscle quite close to the temporal artery and the nervus maxillaris nervus facialis of Fischer (27). In the posterior part of its course it is sinusoidal in character, and the two vessels are probably connected by anastomosing trunks. It is probably the vessel termed supra-orbitalis by Vogt and Jung (78), and its opening was noted by Weber (80), who did not appreciate its significance, thinking it merely a short backward extension of the sinus.

B. XV. *Vena frontalis* (Bruner) (text-fig. 8).—The frontal vein is formed by the union of anterior and posterior rami, which perforate the frontal bone and unite beneath it near the fronto-parietal suture to form a single vessel. This vein runs laterad of the taenia marginalis (Gaupp, 32) and enters the postero-mesial part of the orbital sinus. It drains the tissues overlying the frontal bone.

B. XVI. *Vena maxillaris* (Bruner) (text-fig. 8).—The maxillary vein joins the orbital sinus at its postero-lateral corner. It passes outwards and then forwards in the body of the maxilla between it and the jugal; from the substance of the maxilla and its teeth it receives tributaries. Just before it enters the maxilla the labial vein (XVI. $\beta$) and the jugal vein (XVI. $\alpha$) join it. In the region below the nasal capsule it comes out on to the external surface of the maxilla, and it receives in this part of its course two sets of anastomosing vessels, the one putting it into communication with the nasal sinus (B. XIX. $\alpha$), and the other leading to the anterior network of the lateral palatine sinus (*vide supra*). Just beyond this it receives a small sinus, putting it into communication with the transverse palatine sinus (B. XII. $\alpha$ (i)), and finally it is joined again by the labial vein and immediately runs into the rostral vein (B. XX).

B. XVI. $\alpha$. *Vena jugalis* (Bruner) (text-fig. 8).—The jugal vein is a small twig coming from the tissues in the angle of the mouth.

B. XVI. $\beta$. *Vena labialis superior* (Bruner) (text-fig. 8).—As pointed out above, the labial vein joins the maxillary just as it leaves the posterior end of the maxilla, and bending sharply round this bone runs forward in the upper lip. It drains the skin and subcutaneous tissue as it goes along, and rejoins the maxillary as the latter enters the rostral vein.

B. XVII. *Vena nasalis dorsalis* (Bruner) (text-fig. 8).—The dorsal nasal vein is a small trunk that opens into the antero-mesial region of the orbital sinus. It draws blood from the skin and subcutaneous tissue above the nasal bones through which it passes.

B. XVIII. *Sinus membranæ nictitantis* (BRUNER) (Plate 7, fig. 2, text-fig. 8).—This sinus, which discharges into the anterior part of the orbital just laterad of the orbito-nasal sinus, lies partly in the nictitating membrane and partly in the Harderian gland, into whose substance it penetrates. It also probably receives twigs from the upper eyelid.

B. XIX. *Sinus orbito-nasalis* (Vena orbito-nasalis, GAUPP) (text-fig. 8).—The orbito-nasal sinus is a fairly large sinusoidal vessel, continuing on from the antero-mesial portion of the orbital sinus and draining the large nasal sinus (B. XIX. *α*), through a large foramen in the orbito-nasal septum. It anastomoses with the maxillary vein in the same region as the latter anastomoses with the lateral palatine sinus.

BRUNER does not describe a similar vessel in *Lacerta* nor in *Tropidonotus*, and, in my own observations (58), I was unable to find this vein in the snake. He states that the nasal sinus discharges by means of a sinus lateralis nasi into the maxillary vein. As just noted, this connection also exists in *Sphenodon*, not as a single vessel, but a series of veins. In *Sphenodon*, however, there is no doubt that the main drainage of the nasal sinus is *vid* the orbito-nasal sinus. It is not easy to see why there is this difference between *Sphenodon* and *Lacerta*, unless it be that, in the latter form, where the orbit and nasal capsule are relatively further apart, this connection has been lost. It may probably be regarded as more primitive, since it occurs in the Amphibia as the orbito-nasal vein, GAUPP (31), and in *Scyllium*, O'DONOGHUE (59).

B. XIX. *α*. *Sinus nasalis* (Sinus vestibuli nasi, BRUNER) (text-fig. 8).—The nasal sinus of *Sphenodon* consists of a complex network of anastomosing veins of varying sizes. It ramifies intimately through the peculiar spongy tissue of this region described by LEYDIG (52) and BORN (15) in Lacertilia, who point out its likeness to erectile tissue. In this tissue, in *Sphenodon*, OSAWA (63) first noted the presence of smooth muscle fibres, a point later emphasised by BRUNER (18) in *Lacerta*, and one I am able to confirm. As previously stated, the nasal sinus communicates with the maxillary vein, and apparently with the transverse palatine sinus at its anterior end.

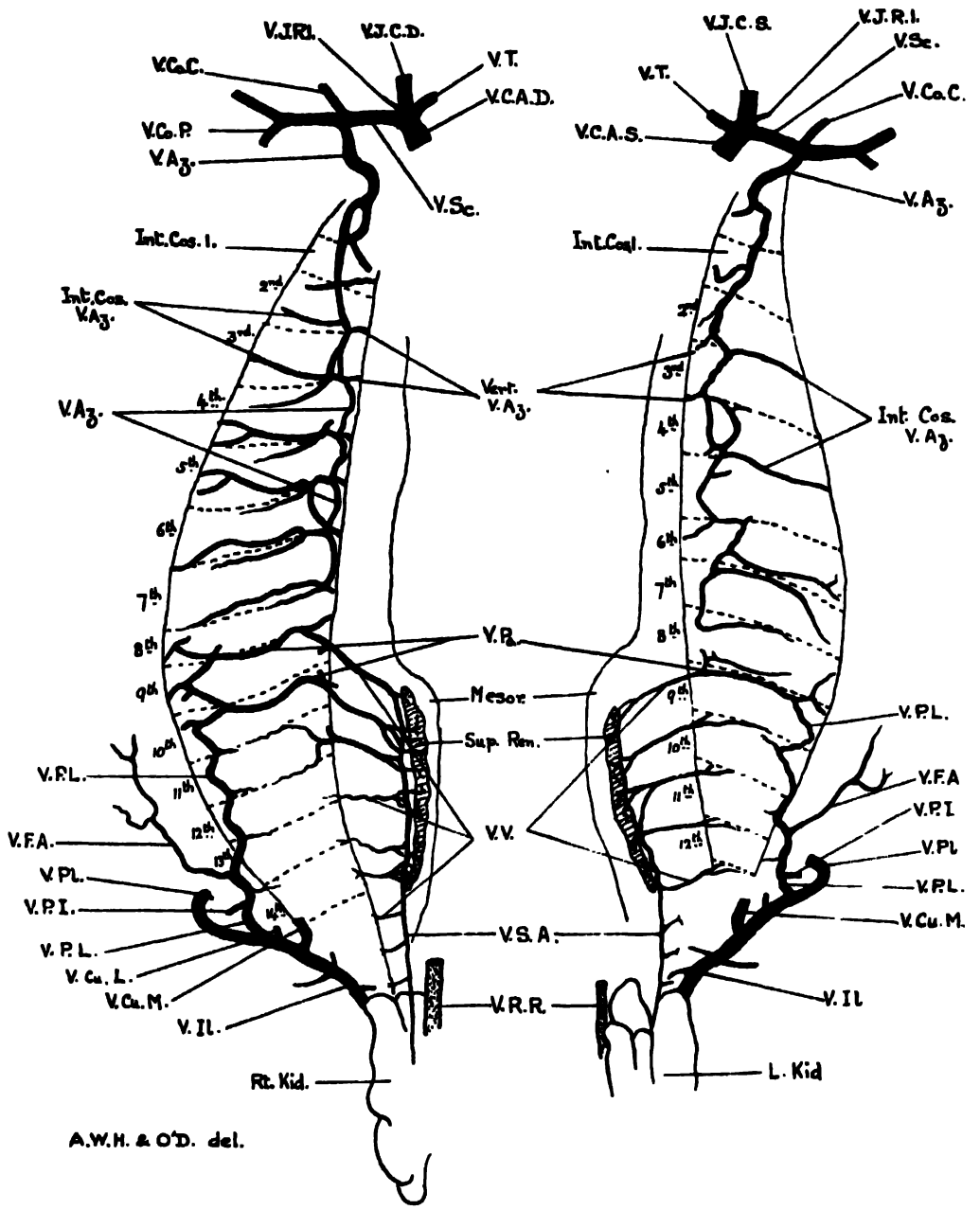
B. XX. *Vena rostralis* (BRUNER) (text-fig. 8).—The rostral vein is a small, irregular transverse vein surrounding the pre-nasal cartilage, and formed by a number of small twigs from the surrounding tissues. At its sides it opens into the maxillary veins in the manner already described, and so not only places them in communication with each other, but also is itself connected through them with the labial vein and transverse palatine sinus.

C. *Vena subclavia* (CORTI) (Plate 6, fig. 1; Plate 7, fig. 2, text-figs. 7 and 9).—The subclavian is the third of the great anterior veins that unite to form the

pre-caval vein. It drains the fore limb, and, in addition, receives factors from the shoulder girdle and the ventral and dorsal body wall. Very little is known about the veins of the limbs in the Lacertilia, save a quite brief account of *Uromastix spinipes* given by Hochstetter (46), with which the present account does not entirely agree, and I know of no reference to them in *Sphenodon*. They differ considerably from *Rana*, where, as has been fully described by Gaupp (31), two large venous trunks come from the upper arm, the brachial and the subclavian, so that it is hard to draw homologies between the two animals, and, as might be expected, *Sphenodon* differs considerably from the mammal. The subclavian is a large trunk that runs straight outwards from its point of union with the jugular and tracheal. A short distance along it receives on its anterior wall a factor (C. I) from the pectoral girdle, and the Azygos (C. II) enters it on the opposite side. About an equal distance further out it receives posteriorly another well-marked factor from the pectoral girdle (C. III), after which it may be termed the Vena axillaris. Just before entering the limb, the great cutaneous vein (C. IV) runs into it on the antero-dorsal side, and the main trunk, passing into the arm, becomes the vena brachialis. On its way to the elbow, along the superficial internal side of the upper arm, three large tributaries (C. V–VII) join it, and, after passing that joint, it becomes the vena antibrachialis superficialis of Gaupp. This passes slowly across the extensor side of the fore arm to its radial border, again receiving three well-marked branches (C. VIII–X), and, at the base of the hallux, turns mesiad, to form the arcus venosus dorsi manus. The arcus first gives off a vessel (C. XI) that anastomoses with its own distal extremity on the ulnar side, and then a series of venæ interdigitales (C. XII) to the spaces between the digits. Finally, it runs round on to the flexor side of the fore arm, and a short way up towards the elbow again, along the outer border of the "Anconæus quartus (richtiger quintus)" muscle of Osawa.

C. I. *Vena coraco-clavicularis* (text-fig. 9).—The coraco-clavicular vein enters the anterior wall of the subclavian about 1 cm. before it flows into the anterior vena cava. It drains the dorsal part of the shoulder girdle, and passes ventrally between clavicle and coracoid and between the costo-scapularis and costo-coracoideus muscles. It receives a factor from the clavicular region.

C. II. *Vena azygos* (Beddard; V. vertebralis posterior, Hochstetter) (text-fig. 9).—The azygos is a large interesting vein, entering the posterior wall of the sub-clavian nearly or quite opposite the coraco-clavicular. It can be traced backwards on both sides of the body to the posterior border of the seventh intercostal space. The factors joining it come from both the costal and vertebral regions, so that the territory it drains corresponds with that




TEXT-FIG. 9.—Dissection of Azygos, Iliac, Afferent Supra-Renal and Associated Veins on both sides.

*Veins.*—*Int.Cos.Az.*, intercostal branches of vena azygos; *V.Az.*, vena azygos; *V.C.A.D.*, vena cava anterior dextra; *V.C.A.S.*, vena cava anterior sinistra; *V.Co.C.*, vena coraco-clavicularis; *V.Co.P.*, vena coraco-pectoralis; *V.Cu.L.*, vena cutanea lateralis; *V.Cu.M.*, vena cutanea magna; *Vert.V.Az.*, vertebral tributaries of vena azygos; *V.F.A.*, vena flexoris abdominalis; *V.J.C.D.*, vena jugularis communis dextra; *V.J.C.S.*, vena jugularis communis sinistra; *V.J.R.I.*, ramus muscularis of vena jugularis communis; *V.Pa.*, venæ parietales; *V.P.I.*, vena pubo-ischio-trochanterica; *V.Pl.*, vena pelvica; *V.P.L.*, vena parietalis lateralis; *V.R.R.*, venæ renales revehentes; *V.S.A.*, vena supra-renalis advehens; *V.Sc.*, vena subclavia; *V.T.*, vena trachealis; *V.V.*, vena vertebralis.

*Int.Cos.*1., first intercostal space; 2nd–14th, second, &c., intercostal spaces; *L.Kid.*, left kidney; *Mesor.*, mesorchium; *Rt.Kid.*, right kidney; *Sup.Ren.*, dorsal surface of supra-renal body.

of the posterior cardinal of the embryo, and there is little doubt it is the actual remains of the anterior part of this. The posterior part of the embryonic post-cardinal probably persists as the afferent supra-renal, as will be discussed later. The break between the two is a very slight one in *Sphenodon*, for the factors of the latter vessel commence in the eighth intercostal space. There is, as far as can be seen, no actual connection between them such as HOCHSTETTER states he has found in Lacerta (46), and furthermore, I have not been able to find one or more venæ hepaticæ advehentes running from the azygos to the portal veins such as are described by the same author.

One of the earliest descriptions of this vessel in Lacertilia we owe to JOURDAIN (49), who describes it as "étendue depuis la jugulaire antérieure jusqu'à la queue," a description that is hardly accurate. According to PARKER (64), it is present only on the right side in *Lacerta viridis*, and this is perhaps substantiated by HOCHSTETTER (*loc. cit.*, p. 457), who terms it the vena vertebralis posterior, and says: "Das Blut aus der linkseitigen V. vertebralis posterior wird durch eine in dieser Gegend stärker entwickelte Queranastomose, von der bereits oben die Rede war, der V. vertebralis dextra zugeführt." The description of this author is not clear, however, for on the same page he apparently calls the vessel the A. vertebralis posterior and seems to suggest it is present on both sides.

Considerable variation in the presence and size of this vessel and the extent of its development on the two sides of the body is to be encountered in the Lacertilia, as has been shown mainly by BEDDARD. It may be present on both sides, and then, as a rule, one is considerably larger than the other. The better developed one may be on the left, as in *Varanus griseus* (8), *Iguana tuberculata* (2), and *Chamæleo sp.* (4), or on the right, as in *Pygopus lepidopus* (4). In yet other cases the vein is absent altogether on one side; the right in *Ophisaurus apus* (*Pseudopus pallasii*) (7); the left in *Phelsuma madagascariensis*, *Tarentola annularis* (4), and in *Heloderma suspectum* (8). The condition in *Sphenodon* is of interest because it is a primitive one, from which that found in any of the Lacertilia can be derived. In the first place, the two vessels are much more nearly of a size than in other forms, and, in the second, they extend back farther than most species, even where the two vessels are present in a fairly marked manner.

C. III. *Vena coraco-pectoralis* (V. thoracica anterior? HOCHSTETTER) (text-fig. 9). —This vessel comes from the ventral portion of the shoulder girdle and enters the sub-clavian vein laterad of the Azygos. The main trunk, which perhaps is homologous with the anterior thoracic of HOCHSTETTER, although it is not the only vessel coming from the girdle, may be regarded as the one passing out to drain the dorsal surface of the coracoideus and adjacent

muscles. It receive two tributaries, one from the pectoralis muscle (C. III. $\alpha$), and one from the sterno-coracoideus (C. III. $\beta$).

C. III. $\alpha$. *Ramus pectoralis.*—The pectoral branch drains the dorsal surface of the pectoralis muscle and also picks up a well marked tributary from the ventral surface of the same.

C. III. $\beta$. *Ramus sterno-coracoideus.*—The sterno-coracoid branch comes from the internus superficialis and internus profundus portions of the similarly named muscle.

The main trunk may now be termed the *Vena axillaris*, as it accompanies the axillaris nerve.

C. IV. *Vena cutanea magna* (BETHGE) (Plate 8, fig. 8).—This vein enters the dorso-lateral extremity of the vena axillaris immediately before that vessel becomes the branchial vein. It comes in through the dorsal shoulder muscles from the external surface of the latissimus dorsi muscle, where it receives a small anterior tributary (C. IV. $\alpha$). The main trunk passes backwards in the latero-dorsal subcutaneous tissue to the region of the pelvis, where it again dives through the musculature to enter the pelvic vein, thus forming a factor (A. III) of the system of the anterior abdominal vein (*q.v.*). This posterior connection is not quite the same as that described by BETHGE (11) in *Salamandra* and *Triton*, but the vessel appears from its general relation and distribution to be the same, so that I have adopted BETHGE'S term of great cutaneous vein. It is not improbable that it will prove to be also homologous with the lateral cutaneous vein of the Elasmobranch (59).

C. IV. $\alpha$. *Vena cutanea parva* (BETHGE).—The small cutaneous vein joins the great vein in the subcutaneous tissue dorsad of the latissimus dorsi muscle. It drains the tissue in the anterior continuation of the same line as the great vein and can be traced forwards to just behind the head.

The main trunk now enters the posterior aspect of the upper arm and so may be termed the *Vena brachialis* (Plate 8, figs. 7 and 8).

C. V. *Vena profunda brachii* (GAUPP) (Plate 8, figs. 7 and 9).—This is obviously not quite the same vessel as the profunda brachii of the frog, since in this animal the vein is a continuation of the subscapular, but as it has a very similar distribution it appears to be justifiable to give it the same name. It drains the cleido-humeralis, supra-coracoideus, anconæus and adjacent muscles, and receives near its end the Vena anastomotica longa (C. X).

C. VI. *Ramus muscularis* 1.—This branch runs into the radial side of the brachial vein just at the elbow, and comes mainly from the ends of the supinator and extensor digitorum communis longus muscles.

C. VII. *Ramus muscularis* 2.—This is the second muscular branch at the elbow, and it passes outwards superficially to the distal end of the anconæus and neighbouring muscles.

The main trunk now passes into the fore arm as the *Vena antibrachialis superficialis* of GAUPP, and is obviously the same vessel as that described by HOCHSTETTER (46) in *Uromastix* as "Eine veine im Sulcus radialis antibrachii" (Plate 8, figs. 7 and 9).

C. VIII. *Vena interossea* (GAUPP) (Plate 8, figs. 7 and 9).—The interosseal vein, probably the "Ulnare Randvene" of HOCHSTETTER, is a fair sized trunk coming off the superficial antibrachial, passing round on to the flexor surface of the proximal end of the radius and over towards the ulnar side of the limb. It runs down deep in the muscles, draining the flexor carpi ulnaris and pronator quadratus, into the hand. Unfortunately it could not be followed satisfactorily, but it appears to receive certain interdigital volar veins and to be connected with the main vessel on the extensor side by anastomoses, one of which is in the region of the bone of the hallux (*vide infra*).

C. IX. *Vena prahallucis* (GAUPP) (Plate 8, fig. 7).—This vein leaves the superficial antibrachial near the carpus and passes to the outside of the thumb, where it probably anastomoses with the veins on the palmar surface of the hand as just noted.

C. X. *Vena anastomotica longa* (Plate 8, fig. 7).—This long anastomosing vein comes off from the main vessel in the region of the distal end of the extensor carpi radialis longus muscle and runs right back up the fore arm and upper arm, following a course roughly parallel with that of the main trunk, but quite superficial. It flows into the brachial vein *viâ* the end of the vena profounda brachii (C.V) near the proximal end of the anconæus.

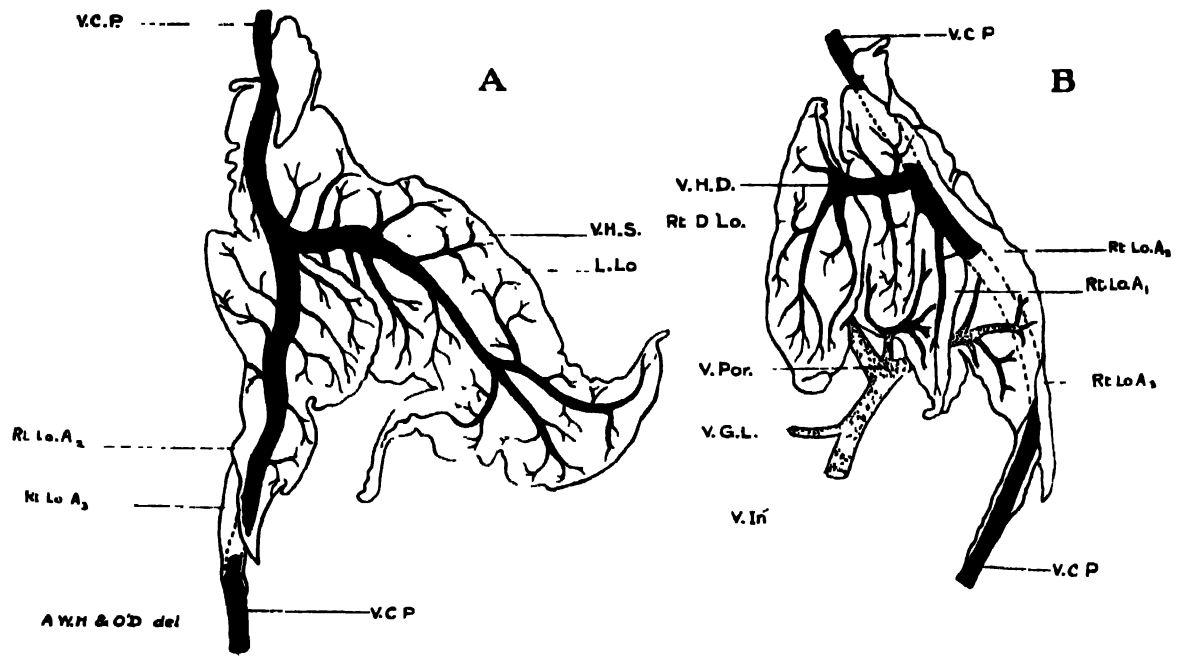
The main trunk now begins to turn across to the ulnar side of the hand, forming a well marked *arcus venosus dorsi manus*.

C. XI. *Vena anastomotica arcus venosi* (Plate 8, fig. 7).—This anastomosing branch comes off from the arcus venosus on the radial side and runs over the back of the hand, to enter the arcus again on its ulnar side.

C. XII. *Venæ interdigitales* (Plate 8, fig. 7).—Four well-marked interdigital veins are received by the arcus, each formed by the union of two lateral digital veins at the base of the space between each respective pair of digits. The fifth vein, corresponding to these, drains the external side of the fifth digit.

*Vena cava posterior* (Plate 6, fig. 1, text-figs. 10 and 11).—The post-caval vein is a large thin-walled trunk lying in the dorsal mesentery slightly to the right of the

middle line and continuing in the line of the right efferent renal vein. It is formed by the union of two efferent renals (E) at the level of the posterior end of the left testis and passes forwards to the attenuated extremity of the right lobe of the liver. Partly embedded in this organ the vessel runs forward to its anterior end, receiving on its way a number of small hepatic veins and two much larger ones, a right (A) and a left (B). In front of the liver the post-caval vein passes freely forward in the mesentery to enter the posterior end of the sinus venosus. Posterior to the liver it receives the right spermatic vein (C), while the left spermatic vein (D) opens into the short anastomosis running transversely between the ends of the efferent renal veins.




TEXT-FIG. 10.—(*a*) Ventral aspect of Liver to show Post-Caval and Left Hepatic Veins. (*b*) Right side of Liver to show Post-Caval, Right Hepatic and Hepatic Portal Veins. The junction of the anterior gastric and anterior abdominal veins with the hepatic portal is hidden by the lobes of the liver.

*Veins.*—*V.C.P.*, vena cava posterior; *V.G.L.*, vena gastero-lienalis; *V.H.D.*, vena hepatica dextra; *V.H.S.*, vena hepatica sinistra; *V.In.*, vena intestinalis; *V.Por.*, vena portæ.

*Rt.D.Lo.*, right dorsal lobule of liver; *Rt.Lo.*, A 1, A 2, and A 3, the three right ventral lobules of liver; *L.Lo.*, left lobe of liver.

A. *Vena hepatica dextra* (text-fig. 10).—The right hepatic vein is a fair-sized vessel composed of a number of factors from the various lobes of the liver on the right side. It enters the post caval about 3·5 cm. behind the point where this vessel leaves the anterior end of the liver.

B. *Vena hepatica sinistra* (text-fig. 10).—The left hepatic vein is smaller but very similar to the right, save that it comes from the left lobes of the liver and enters the left wall of the post caval just caudal to the point of entry of the right hepatic vein.

C. *Vena spermatica dextra* (Plate 6, fig. 1, text-fig. 11).—The right spermatic vein arises as a network of small vessels in the mesorchium at the anterior end of the testis. It then runs backwards along the supra-renal bodies, which it almost covers, receiving the efferent supra-renal veins (C. I), and also receiving as a rule four fair-sized veins from the testis. At the posterior end of the testis it turns sharply inwards and flows into the post-caval vein.

C. I. *Venæ supra-renales revehentes.*—These are a series of minute twigs coming from the supra-renal body, opening into the spermatic vein during its course along that gland and serving as efferent supra-renal veins.

D. *Vena spermatica sinistra* (Plate 6, fig. 1, text-fig. 11).—The relations of the left spermatic vein to the corresponding supra-renal body and testis are similar to those on the right, save that, as a rule, it has five branches from the testis instead of four. It does not open directly into the post-caval vein, but into the transverse anastomosis joining the left efferent renal to the right.

D. I. *Venæ supra-renales revehentes.*—A series of efferent supra-renal veins, similar to those on the right, open into the left spermatic vein.

E. *Venæ renales revehentes* (HOCHSTETTER) (Plate 6, fig. 1, text-fig. 11).—The efferent renal veins commence in the substance of the kidneys at their posterior ends and run forward as fair-sized thin-walled vessels on the median borders of their ventral faces and separated from one another in the middle line by the dorsal mesentery. The right vein, from the start, is much larger than the left, a condition that is common in the Lacertilia (*vide* BEDDARD, 7), and the two are joined by four large inter-renal anastomoses. Herein *Sphenodon* differs from both *Lacerta viridis*, *L. ocellata*, and *Varanus arenarius*, in which, according to HOCHSTETTER (46), there is only one small anastomosis at the posterior end of the kidneys. Between the kidneys and the place where they join one another, both veins receive a number of small tributaries from the mesentery. As already stated, the left efferent renal pours its blood into the right at the level of the hinder end of the left testis, by means of a short stout anastomosis into which the left spermatic vein runs.

The remaining veins of the body are not concerned with taking the blood back directly to the heart, and so can be dealt with conveniently as a series of distinct but often closely related systems.

### *The Supra-renal Portal System.*

The presence of this system has already been noted in the *Varanidæ* by CORTI (21), HOCHSTETTER (46), and BEDDARD (8), in which genus it is very well developed. It is subject to a great deal of variation in the Lacertilia, as BEDDARD has shown, and, although usually present and often well marked, as in the *Varanidæ*, *Iguana*

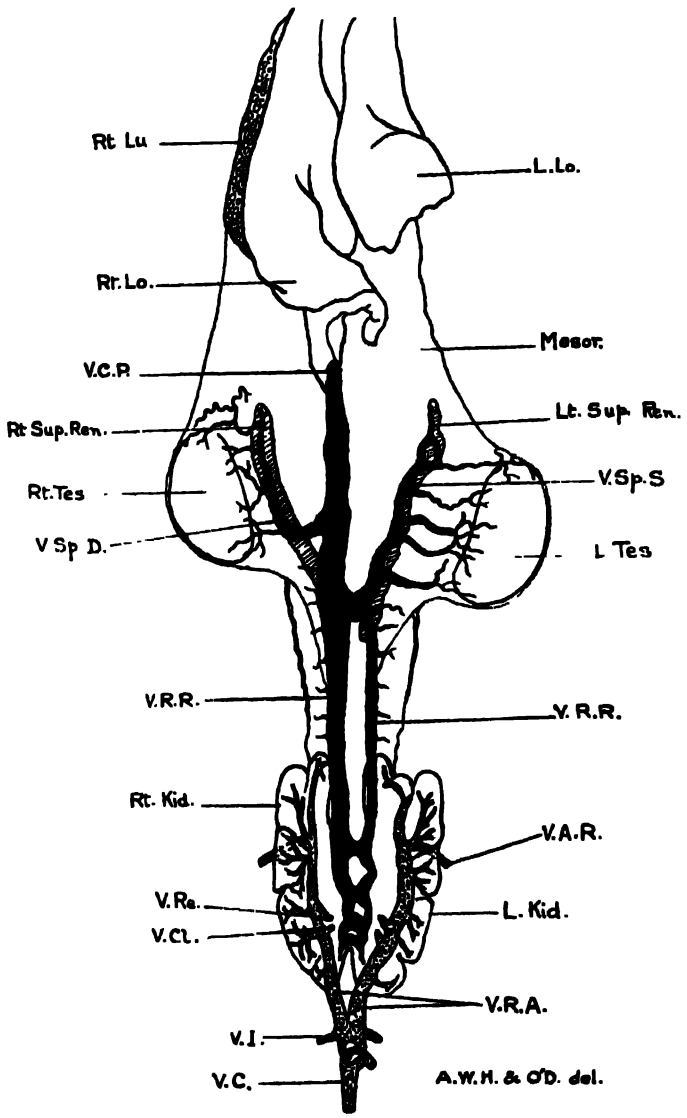
*tuberculata* (2), *Ophisaurus apus* and *Amphisbæna brasiliana* (7),* it may be considerably reduced, *e.g.*, *Tiliqua scincoides* (2), or even absent altogether, save as an abnormal variation, as in *Chamæleon vulgaris* (4). In *Sphenodon* it has apparently retained more primitive relations than in the other forms described, and this throws useful light on the question of its constitution. Its main factor is a vessel, termed by HOCHSTETTER (46) the Vena deferentialis, since it accompanies the vas deferens, and by BEDDARD (7) the post cardinal vein. With regard to this vessel, BEDDARD, after pointing out that it receives branches from the parietes, adds: "Considering . . . the relation of the vein to the vas deferens (Wolffian duct), I imagine that it is to be regarded as a persistent, though small, posterior cardinal vein." The position of the vessel in *Sphenodon*, I think, fully supports this interpretation. The azygos vein, Vena vertebralis of HOCHSTETTER, is generally admitted to be a persistent part of the embryonic posterior cardinal vein, and it receives factors not only from the parietes, but also from the vertebral region. It will be seen that the vein in question similarly has parietal and vertebral branches at its anterior end, and, indeed, the break between it and the azygos on both sides is very small, being only from one vertebra to the next. In *Lacerta viridis*, as figured by HOCHSTETTER, it would appear as if there is not even this hiatus. Moreover, the posterior end of the vein disappears in the kidney substance as the old posterior cardinal would. Then again, in *Varanus arenarius*, HOCHSTETTER (*loc. cit.*, Plate 16, fig. 16) depicts the vein as opening into the anterior end of the afferent renal, and so directly continuous with the caudal vein. There seems to be little doubt, then, that this vessel is actually a persistent, though much reduced, portion of the posterior cardinal vein.

A. *Vena supra-renalis advehens* (V. cardinalis posterior, BEDDARD; V. deferentialis, HOCHSTETTER) (text-fig. 9).—The term afferent supra-renal vein seems preferable to posterior cardinal, as employed by BEDDARD, since the vessel is only a small part of the embryonic posterior cardinal, while the azygos is a larger persistent portion of the same trunk, and so more deserving of the name. The term vena deferentialis of HOCHSTETTER is open to the objection that it is obviously unsuitable in the case of the female. Afferent supra-renal is free from both these objections, and at the same time indicates its anatomical relation to the supra-renal gland by pairing it with the efferent supra-renal veins. In *Sphenodon* the vessel arises in the anterior end of the kidney, and passes forwards alongside the vas deferens to the anterior end of the supra-renal body to the substance, of which it gives off a large number of small twigs. Along its course it receives factors from the vertebral region (A. I), and also from the parietes (A. II).

* This vessel does not appear to be present in a female *Amphisbæna cinerea* examined by V. BEDRIAGA (9). He figures the parietal veins from this region of the body as opening directly into the efferent renal veins.

A. I. *Venæ vertebrales* (text-fig. 9).—The vertebral veins come from the region of the vertebræ. There are nine of them on the right side and eight on the left, opening into the afferent supra-renal vein, and the anterior vessels on each side are connected with the corresponding parietals.

A. II. *Venæ parietales* (text-fig. 9).—On the right side are two large parietal veins which unite with their corresponding vertebrals, and, by means of the common trunk so formed, drain into the afferent supra-renal. At their




TEXT-FIG. 11.—The Post Caval, Renal Portal, Renal Efferent and Spermatic Veins, and their connections.

*Veins.*—*V.A.R.*, vena anastomotica renalis; *V.C.*, vena caudalis; *V.Cl.*, vena cloacalis; *V.C.P.*, vena cava posterior; *V.I.*, vena inguinalis; *V.R.A.*, venæ renales advehentes; *V.Re.*, vena rectalis; *V.R.R.*, venæ renales revehentes; *V.Sp.D.*, vena spermatica dextra; *V.Sp.S.*, vena spermatica sinistra.

*L.Kid.*, left kidney; *L.Lo.*, left lobe of liver; *Lt.Sup.Ren.*, left supra-renal body; *L.Tes.*, left testis; *Mesor.*, mesorchium; *Rt.Kid.*, right kidney; *Rt.Lo.*, right lobes of liver; *Rt.Lu.*, right lung; *Rt.Sup.Ren.*, right supra-renal body; *Rt.Tes.*, right testis.

distal extremity these two parietal veins open into the lateral parietal vein, so forming well marked anastomoses between it and the afferent supra-renal, placing the supra-renal portal system into communication with the system of the caudal vein. On the left side there is only one similarly constituted vein.

The next two right parietal veins are reduced, and join together before uniting with the vertebral. The parietal factors on both sides caudad of those described get so much reduced that they practically disappear.

*The System of the Caudal Vein* (text-fig. 11).

This system forms in the main a portal system to the kidneys, *i.e.*, most of the blood brought by it passes through the substance of the kidneys, and is returned to the heart by way of the efferent renal veins.

A. *Vena caudalis* (text-fig. 11).—The caudal vein commences far back in the tail, and runs forward in the hæmal arches, receiving paired factors from the muscle segments on its way. Just before reaching the hinder end of the kidneys it becomes swollen, receives veins from the inguinal region (A. I), and shows a tendency to split into two. Finally, it does divide into two veins, which diverge and enter the posterior ends of the kidneys, becoming the afferent renal veins (B).

A. I. *Vena inguinalis* (text-fig. 11).—The inguinal vein is a well marked vessel on each side bringing in blood from the inguinal region.

B. *Vena renales advehentes* (text-figs. 11 and 13).—The right afferent renal or Jacobson's vein is generally smaller than the left. They both enter the posterior ends of the corresponding kidneys and run forward, partially buried in the kidney substance in its mid-ventral line. Each receives a cloacal (B. I) and a rectal factor (B. II). The vessel gradually diminishes in size, breaking up in the kidney. It sends a fair sized branch in the deep cleft between the first and second kidney lobes which turns dorsally and enters the iliac vein, thus establishing a direct connection between the systems of the caudal and abdominal veins. BEDDARD (7, p. 464) states that in *Sphenodon* he was unable to find any such connection, and opines that if the two systems are connected at all it is only indirectly through the kidney substance. The vessel, although hidden in a cleft, shows clearly in a well injected specimen, and was also found in the other specimens examined. It is a vein very similar to that figured in *Lacerta* by HOCHSTETTER (46, Plate 16, fig. 12), save that it runs in a cleft in the kidney and not superficially across its ventral surface.

B. I. *Vena cloacalis.*—The cloacal vein is a small tributary from the side of the cloaca entering the afferent renal about 6–8 mm. from the posterior end of the kidney.

B. II. *Vena rectalis.*—The rectal vein comes from the dorsum of the anal gland and receives small factors from the base of the bladder. It enters the afferent renal just anterior to the cloacal vein.

The following three systems are, strictly speaking, all parts of the one hepatic portal series of veins, since they all take blood to the liver. For convenience, however, they may be treated separately and dealt with as a main hepatic portal system with two closely related accessory systems, that of the anterior abdominal vein and that of the epigastric veins.

### *The Hepatic Portal System* (text-figs. 10 and 12).

This system is, on the whole, similar to that in *Lacerta viridis* and figured by HOCHSTETTER (*loc. cit.*, Plate 16, fig. 15). It differs mainly in the fact that it has a large anterior gastric factor, which itself gives off a number of portal branches directly to the liver.

A. *Vena porta* or *Vena hepatica advehens* (HOCHSTETTER) (text-figs. 10 and 12).—The hepatic portal vein is quite a short trunk formed mainly by the union of the lieno-gastric (A. I) and intestinal (A. II) veins, and is distributed mainly to the right lobes of the liver, while the left lobes of the liver are supplied almost entirely by the anterior gastric factor (A. III).

A. I. *Vena gastero-lienalis* (HOCHSTETTER) (text-fig. 10).—The lieno-gastric vein is formed at the anterior end of the spleen, when a number of small factors and one larger one (A. I. $\beta$) from that body join a small gastric vein (A. I. $\alpha$). It is soon joined by another small gastric tributary (A. I. $\gamma$) and runs in the mesentery alongside the pancreas, from which it receives a vessel (A. I. $\delta$). Finally it joins the intestinal vein in the neighbourhood of the pylorus, from which part of the gut it also receives blood (A. I. $\epsilon$).

A. I. $\alpha$. *Vena gastrica* 1.—The first gastric vein is a small vessel arising from the left hand side of the stomach about half-way down. It runs freely in the lieno-gastric omentum, and at the anterior end of the spleen receives from that body six or eight small veins.

A. I. $\beta$. *Vena lienalis.*—The splenic vein is a trunk formed by the union of a number of small factors from the posterior end of the spleen, and after a short course it unites with the first gastric vein to form the lieno-gastric.

A. I. $\gamma$. *Vena gastrica* 2.—The second gastric vein is another small vessel coming from the caudal end of the cardiac part of the stomach and entering the lieno-gastric shortly after this leaves the spleen.

A. I. $\delta$. *Venæ pancreaticæ.*—As the main trunk passes the pancreas a number of small tributaries from that gland flow into it.

A. I. $\epsilon$. *Vena pylorica.*—The pyloric vein is constituted by the union of a

number of a small branches from the region of the pylorus, and it joins the main trunk just before it enters the intestinal.

A. II. *Vena intestinalis* (text-fig. 10).—The intestinal vein commences low down on the rectum as a rectal vein, and leaving its cranial end runs forward in the mesentery to unite with the lieno-gastric. During its path through the mesentery two tributaries from the intestine (A. II. $\beta$ and $\gamma$) and one from the duodenum (A. II. $\alpha$) flow into it.

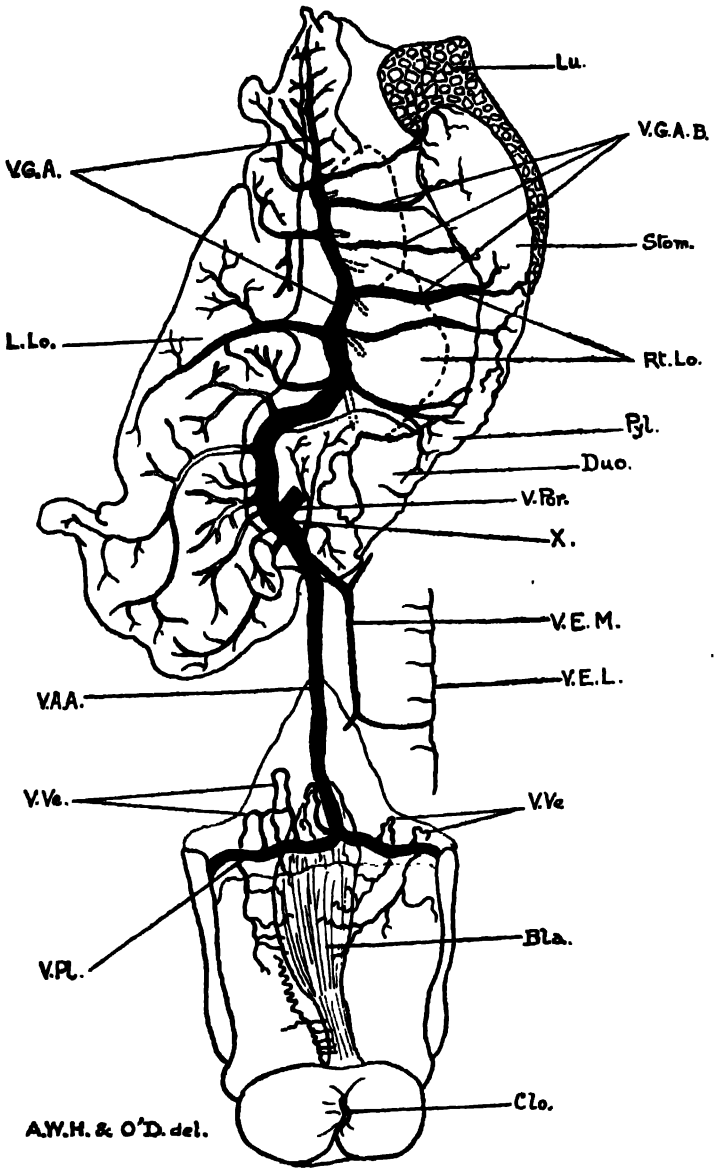
A. II. $\alpha$. *Vena duodenalis.*—The duodenal vein is composed of several branches from the duodenum, which unite to form a single vessel entering the intestinal vein just before it joins the lieno-gastric.

A. II. $\beta$. *Vena intestinalis anterior.*—The front end of the intestine is drained by the anterior intestinal vein, which enters the main intestinal vein as it passes through the mesentery.

A. II. $\gamma$. *Vena intestinalis posterior.*—The posterior intestinal vein comes from the remaining and hinder part of the intestine as far back as the rectum. It reaches the main trunk a short distance caudal of the anterior intestinal vein.

A. III. *Vena gastrica anterior* (text-fig. 12).—The anterior gastric vein is a large vessel originating in the gastro-hepatic omentum near the anterior end of the stomach in a twig coming from that organ. It passes backwards close to the left lobe of the liver, receiving five or six large tributaries coming from the whole of the stomach back to the duodenum. Near the end of that lobe of the liver it bends in suddenly to enter the main hepatic portal trunk as this enters the right liver lobes. Just at the point where it turns it receives the large anterior abdominal vein (A. III. $\alpha$); indeed, it appears as if it were a continuation of that vessel, as a glance at the text-figure (*i.e.*, 12) will show.

BEDDARD, indeed (7, p. 464), regards it as a forward extension of that vein, for he says: "The anterior abdominal vein, reinforced by the portal, runs in the membrane which connects the stomach with the left lobe of the liver, giving off branches to the liver substance and receiving at intervals branches from the stomach. Towards the anterior end of the liver the conjoined porto-abdominal trunk finally disappears in the liver." He instances an example of a similar distribution in a snake, *Eryx* (5), and claims *Pygopus* as showing an intermediate condition (7). In spite of its appearance, however, I think it better to regard this vessel as an anterior gastric factor of the hepatic portal system corresponding to the several gastric veins in *Lacerta viridis* according to HOCHSTETTER (2), which open separately into the liver. The vessel, moreover, is in a similar position to a corresponding gastro-hepatic factor in *Salamandra* and *Triton*, with which it is no doubt homologous. The matter can only be definitely settled, however, by reference to its development, but, of course, there must be some such portal vessel or vessels draining the




TEXT-FIG. 12.—Diagram of the Anterior Abdominal Vein, showing its relation to the Liver, the Epigastric and Hepatic-Portal Veins.

*Veins.*—*V.A.A.*, vena abdominalis anterior; *V.E.L.*, vena epigastrica lateralis; *V.E.M.*, vena epigastrica media; *V.G.A.*, vena gastrica anterior; *V.G.A.B.*, gastric branches of the vena gastrica anterior; *V.Pl.*, vena pelvica; *V.Por.*, vena porta; *X.*, point of entrance of the anterior abdominal vein into the anterior gastric as the latter joins the main hepatic portal trunk.

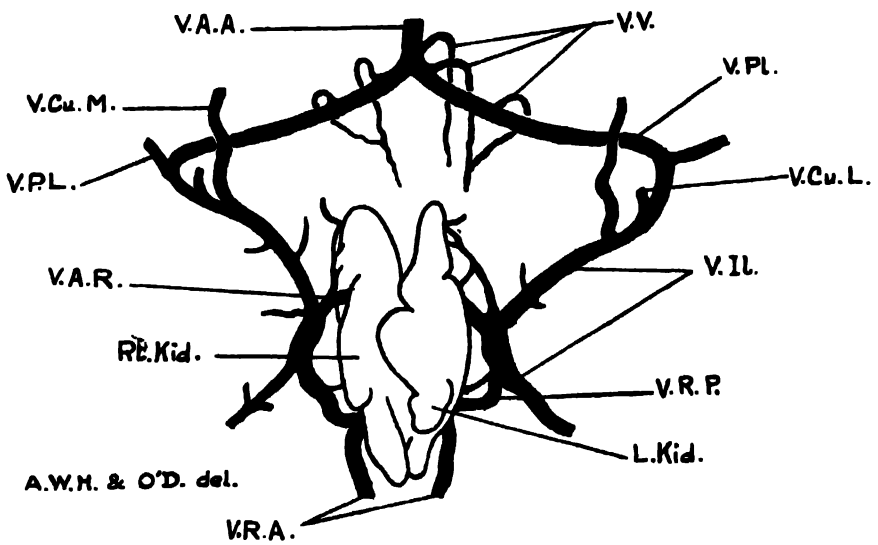
*Bla.*, bladder; *Clo.*, cloaca; *Duo.*, duodenum; *L.Lo.*, left lobe of liver dorsal surface; *Lu.*, lung; *Pyl.*, pylorus; *Rt.Lo.*, right lobes of liver seen through mesentery; *Stom.*, stomach.

stomach before the two lateral abdominal veins have joined to form the single anterior abdominal.

All along its course it gives numerous short venæ advehentes, mostly to the left lobes of the liver, but some also to the right, so that most of its blood

can go straight to the liver substance without entering the main hepatic portal trunk. Indeed, as will be seen, most of the blood from the main portal vessel goes to the right lobes, while the bulk of that from the anterior abdominal vein and the anterior gastric goes to the left lobes.

A. III. *α. Vena abdominalis anterior.*—The anterior abdominal vein, although really only a factor of the anterior gastric, is here treated separately as a matter of convenience.




TEXT-FIG. 13.—The Pelvic Ring, showing the relation of the Iliac, Renal, and Anterior Abdominal Veins. The outer edges of the kidney turned over mesially.

*Veins.*—*V.A.A.*, vena abdominalis anterior; *V.A.R.*, vena anastomotica renalis; *V.Cu.L.*, vena cutanea lateralis; *V.Cu.M.*, vena cutanea magna; *V.Il.*, vena iliaca communis; *V.Pl.*, vena pelvica; *V.P.L.*, vena parietalis lateralis; *V.R.A.*, venæ renales advehentes; *V.R.P.*, vena renalis posterior; *V.V.*, venæ vesicæ.

*L.Kid.*, left kidney; *Rt.Kid.*, right kidney.

*The System of the Anterior Abdominal Vein* (text-figs. 12 and 13).—As has just been pointed out, the anterior abdominal vein opens into the anterior gastric branch of the hepatic portal vein, and so is portal to the liver.

*Vena abdominalis anterior* (HOCHSTETTER) (text-figs. 12 and 13).—The anterior abdominal vein is formed in the mid-ventral line by the union of the two pelvic veins (A), which, in their turn, are continuations of large branches from the common iliac veins (B). Its relations to the common iliac veins and to the afferent renal system is very similar to that in *Salamandra maculosa* as figured and described by HOCHSTETTER (45), and also in *Salamandra*, *Triton* and *Spelerpes* according to BETHGE (11). Although there seems to be a connection between the roots of the anterior abdominal and afferent renal vessels generally in Lacertilia, it varies considerably in different forms, as has been pointed out by HOCHSTETTER (46) and in BEDDARD'S useful series of papers (2–5). It is interesting to find that *Sphenodon*

and *Lacerta* retain the primitive Urodele condition. Just before entering the liver it may receive the epigastric vein (C).

A. *Vena pelvica* (Wurzel der V. abdominalis, HOCHSTETTER; R. abdominalis, GAUPP) (text-figs. 12 and 13).—The pelvic veins may be considered as arising where the common iliac veins anastomose with the afferent renal system, although they are to all appearances direct continuations of the common iliac veins. They pass forward laterally, and then turn in rather sharply ventralwards to unite in the mid-ventral line and give origin to the anterior abdominal vein. During their course each receives a series of factors (A. I–VI).

A. I and II. *Venæ parietales.*—Just as the pelvic vein turns laterally it receives a couple of small factors from the posterior parietes.

A. III. *Vena cutanea magna* (BETHGE) (text-figs. 9 and 13).—The great cutaneous vein arises from the pelvic just in front of the point where this vessel crosses the femoral nerve. It pierces the muscles and passes forwards in the subcutaneous tissue of the latero-dorsal body wall to the scapular region. Here, again, as pointed out above, it leaves its subcutaneous position, and piercing the muscles, flows into the axillaris vein laterally to the azygos vein. In spite of the fact that its posterior connections are somewhat different, it is no doubt homologous with the V. cutanea magna of the Urodela *Salamandra*, *Triton*, etc., as described by BETHGE (11).

A. IV. *Vena cutanea lateralis* (text-figs. 9 and 13).—The lateral cutaneous vein is a smaller but nevertheless well marked vein coming from the skin of the lateral body wall. It joins the pelvic shortly after the great cutaneous vein.

A. V. *Vena parietalis lateralis* (Lateral abdominal, BEDDARD) (text-figs. 9 and 13).—This vein is described by BEDDARD (*loc. cit.*) in a number of Lacertilian forms and appears to be a constant factor of the pelvics, although exhibiting a varying degree of development in different species. It has been termed the lateral abdominal vein, but this term seems open to exception.

In the Elasmobranchs (59) the lateral abdominal vein is a more ventral vessel, running from the iliac forward to the subclavian vein latero-ventrally under the peritoneum on each side. According to MARSHALL (56) in the Tadpole and GOETTE in *Bombinator igneus* (35), these two lateral veins are fused to form the median anterior abdominal vein, which acquires a secondary connection with the hepatic portal system. Certain abnormal adult specimens of *Rana*, BULLER (19), WOODLAND (81), and O'DONOGHUE (57), seem to bear out this account. If, then, this description of the formation of the anterior abdominal vein be correct, the vessel now to be described is not the homologue of the lateral abdominal of the fish. The term lateral parietal

costal space from a parietal vein which connects it with the supra-renal portal system (*q.v.*).

It passes backwards in the angle between dorsal and ventral body wall, receiving small parietal factors from the intercostal spaces. Before entering the pelvic vein it receives two tributaries from the adjacent musculature (A. V. $\alpha$ and $\beta$).

A. V. $\alpha$. *Vena flexoris abdominis.*—This is a moderate sized vessel, flowing into the lateral parietal vein at the level of the hinder end of the thirteenth intercostal space. It drains the flexor abdominis muscle.

A. V. $\beta$. *Vena pubo-ischio-trochanterici.*—This is a smaller vein, coming mainly from the pubo-ischio-trochanticus muscle and joining the lateral parietal vein just before it reaches the pelvic.

A. VI. *Venæ vesicæ* (text-figs. 12 and 13).—There appear to be generally five small vesicular veins, two entering each pelvic vein shortly before its union in the middle line, and the remaining one joining the base of the anterior abdominal.

B. *Vena iliaca communis* (GAUPP; V. ischiadica, HOCHSTETTER) (text-fig. 13).—Although in his second paper (46) HOCHSTETTER terms this vessel the vena ischiadica, there is no doubt it is the same vessel that in the Amphibia he calls vena iliaca (45). The latter name is preferable from the comparative point of view, since the same vessel receives this name in Elasmobranchs (59) and Amphibia (11 and 45), and one of its tributaries is the vena ischiadica of GAUPP (31), and this corresponds most nearly with the similarly named vessel in the Mammalia (*i.e.*, the former sciatic vein of the English anatomists). The common iliac vein is the main trunk draining the whole of the hind limb, after coming in from which it turns forwards and runs along for some distance parallel with the lateral wall of the kidney. It may be regarded as finishing near the front end of that organ, where it passes as a vena anastomotica (B. I), running in a cleft in the kidney into the afferent renal vein. Just at this point, as mentioned above, it gives rise to the large pelvic vein (*q.v.*), which looks like a continuation of the common iliac, but is better regarded as a tributary of it. At the hinder end of the kidney the common iliac sends a well marked tributary into the kidney substance (B. II). From this point it passes out towards the limb, receiving after a very short distance the ischiadic vein (B. III) from the deeper muscles of the external flexor side of the thigh. It now may be termed the *Vena iliaca externa* for a short way until it enters the limb as the *Vena femoralis*. It comes out on to the extensor surface of the thigh from between the ilio-femoralis and ischio-trochantericus muscles and, running mainly beneath the former, passes down to the knee, receiving three branches at its upper end (B. IV–VI). In the

lower part of this course it comes to lie close to the ischiadic artery, and may now be termed the *Vena poplitea*, and a number of branches (B. VII–X) enter it just above or just below the knee. It passes on down the extensor surface of the leg between the peroneus and extensor digitorum communis longus muscles, and may be called the *Vena peronea* down to the end of the body of the latter muscle, where it gives off a branch (B. XI), and runs on to the dorsal surface of the foot as the *Vena dorsalis pedis*. This forms an *Arcus venosus*, receiving a number of veins (B. XII–XV) from the extremity of the foot.

B. I. *Vena anastomotica renalis* (text-figs. 11 and 13).—As already noted, the front end of the iliac vein forms an anastomosing vessel that runs in a deep cleft between the first and second kidney lobes, thus putting the iliac and afferent renal vessels into direct communication. Just before turning mesiad, or just before entering the kidney substance, this vessel receives a factor (B. I. $\alpha$) from the anterior end of the kidney. It is hard to say which way the blood flows in this anastomosing vein without an observation on a living specimen.

B. I. $\alpha$. *Vena renalis anterior*.—This is a small factor, composed of several twigs from the first kidney lobe, and, from its constitution, looks as if it were efferent from the kidney.

B. II. *Vena renalis posterior* (text-fig. 13).—The posterior renal vein leaves the iliac and runs to the hinder kidney lobes, often giving off a fine vessel to that organ, before entering it. The direction of flow in this vessel also is not apparent, although it may be afferent to the kidney. It is not improbable that the direction of flow in both this and the preceding vein may vary in correlation with the relative changes of venous pressure in the kidney, limbs, and tail.

B. III. *Vena ischiadica* (? GAUPP).—A short distance before entering the limb, the main trunk receives a tributary, which may possibly correspond with the ischiadic vein in the frog, according to GAUPP, although, as he points out, it does not accompany the similarly named nerve. This vessel was not satisfactorily followed as in the examples examined; it was either not injected or did not contain sufficient blood to render it conspicuous. It comes from the deeper muscles on the external flexor side of the limb, and apparently drains the pubo-ischio-femoralis, pubo-ischio-trochantericus externus, pubo-ischio-tibialis and pubo-tibialis muscles, and also the deeper surfaces of the ischio-tibialis posticus and extensor triceps muscles.

The main trunk is now the *Vena iliaca externa* for a short way, and then enters the limb as the *Vena femoralis* (Plate 7, fig. 4; Plate 8, fig. 6).

B. IV. *Vena cutanea* 1 (Plate 8, fig. 6).—The first cutaneous vein is a small superficial factor, joining the main trunk high up between the ileo-femoralis and ischio-trochantericus muscles.

B. V. *Ramus muscularis* 1.—This is a larger vein, joining the femoral a little below the preceding, and composed of two main factors: one from the extensor side of the ischio-tibialis muscle and one from the ischio-tibialis-posticus.

B. VI. *Ramus muscularis* 2.—The second muscular vein is about the same size as the first, and enters about half way down the thigh. It is also composed of two branches, one from the ilio-femoralis and one from the external, lower portion of the extensor triceps muscle.

Some distance below this the main trunk is called the *Vena poplitea* (Plate 7, fig. 4; Plate 8, fig. 6).

B. VII. *Ramus muscularis* 3.—This is a short muscular trunk coming from the lower posterior part of the extensor triceps muscle.

B. VIII. *Vena cutanea* 2.—The second cutaneous vein comes from the superficial tissues close to the knee, and enters the main trunk just above the joint.

B. IX. *Ramus muscularis* 4.—A fairly large muscular branch comes from between the gastrocnemius and peroneous muscles, which it drains, and joins the popliteal vein almost at the knee joint.

B. X. *Vena circumflexa genu lateralis inferior* (Gaupp) (Plate 8, fig. 6).—The circumflex vein corresponds closely with the similarly named vessel in the frog. It enters the popliteal by two short vessels, and drains the tendinous capsule of the knee and the insertion of the extensor triceps muscle.

The main trunk is now termed the *Vena peronea* (Plate 7, fig. 4; Plate 8, fig. 6).

B. XI. *Vena anastomotica arcus venosi* (Plate 8, fig. 6).—The anastomosing vein leaves the end of the peroneal, and runs downwards and mesiad, to enter the mid region of the arcus venosus, just opposite to the interdigital vein of digits three and four.

The main trunk now becomes the *Vena dorsalis pedis* (Plate 8, fig. 6).

B. XII. *Vena circumflexa tarsi* (Gaupp) (Plate 8, fig. 6).—The tarsal circumflex vein passes round over the distal extremity of the peroneus muscle on to the plantar surface of the foot, where it is probably connected with the plantar veins, although these could not be satisfactorily made out. It receives a small twig from the outer side of the fifth digit.

B. XIII. *Venæ interdigitales* (Plate 8, fig. 6).—Three well marked interdigital veins enter the arcus venosus. The first and second come from the spaces between the fourth and fifth and third and fourth digits respectively. The

third is a very short trunk, formed by the union of the two veins related to the space between digits two and three and one and two.

B. XIV. *Vena præ-pollicis.*—This vein runs up the external border of the big toe.

B. XV. *Ramus muscularis* 5.—The muscular vein comes from between the distal ends of the tibialis anticus and extensor digitorum communis longus muscle. It joins with the foregoing to form the distal end of the arcus venosus.

*The System of the Epigastric Veins* (text-fig. 12).—Unfortunately it was not possible to make out the details of the epigastric veins, which are never easy to dissect. They were not successfully injected in any of the specimens, and they are hidden by the dense black pigmentation of the peritoneum. Certain parts of the system, however, were traced fairly satisfactorily. The epigastric veins in the Lacertilia differ very considerably from species to species, according to the observations of Beddard. The most common arrangement is apparently a median epigastric vein running in the mid-ventral line, such a vessel is found, for example, in *Tiliqua scincoides* (2), *Phelsuma madagascariensis* (4), *Heloderma suspectum* (8), and *Ophisaurus apus* (7). When paired or lateral epigastric veins are present their anterior and posterior connections differ so considerably that there is apparently no common arrangement. Paired epigastric veins are present in *Varanus griseus* (8), and in yet other forms, *Iguana tuberculata* (2), *Tupinambis nigropunctatus* (3), and *Chamæleon vulgaris* (4), both lateral and median epigastric veins occur.

*Sphenodon* possesses a well marked median and smaller lateral epigastric veins.

*Vena epigastrica lateralis* (text-fig. 12).—The lateral epigastric vein is a small vessel running in the ventral abdominal wall in the region of the epigastric artery. Just behind the liver it unites with its fellow in the middle line to form the median epigastric vein. The anterior and posterior connections of this vessel could not be ascertained. In the short part of its course, over which it was traced, it was found to receive several small parietal factors. In the case of *C. vulgaris* there is a somewhat similar relation between lateral and median epigastrics, for the two former unite to form the latter, only in this case it is in front of the liver.

*Vena epigastrica media* (text-fig. 12).—The median epigastric vein is a somewhat short but well marked vessel formed, as far as could be seen, by the union of the two factors from the lateral epigastrics, and running forward to the hinder end of the liver. Here the main part of it enters the anterior abdominal vein, just before this joins the hepatic portal, while a smaller part passes on forward in the mid-ventral line, but it could only be followed for a short distance. In *Ophisaurus apus* the median epigastric is in two portions, and the posterior part is related to the anterior abdominal vein in a manner similar to that in *Sphenodon*. When a median epigastric vein is present it is generally related to the anterior abdominal vein.

### *Venæ Pulmonales* (text-fig. 1).

The pulmonary veins are two moderate sized thin-walled vessels running up the ventro-lateral borders of the lungs, one on each side of the body. They increase in size as they receive numerous tributaries from the substance of the lungs themselves. Leaving the anterior end of the lungs they pass dorsally to the sinus venosus, to become closely attached to its anterior border on the atrial walls. As has been pointed out previously, they open into the postero-mesial corner of the left atrium by an aperture partly hidden by a fold of the atrial wall and quite close to the inter-atrial septum.

## Summary.

The heart is on the whole reptilian but of a simple unspecialised type, in which the three main arterial vessels instead of opening directly from the ventricle come off by a short common trunk, possibly a remains of the conus arteriosus.

The arterial system in general is distinctly reptilian, and while in some respects it may recall conditions in other orders of Reptilia, it most closely resembles that of certain Lacertilians, but it is undoubtedly less specialised and shows certain interesting points of similarity with that of the Urodeles.

The same general remarks also apply to the veins, which are more primitive than those of Lacertilia, although they approximate more nearly to the latter than to other Reptiles.

Certain special points in the blood vessels will be summarised below when considering the light they throw upon the position of *Sphenodon* in the class Reptilia. It only remains to note that the blood vascular system of the Tuatara is of considerable anatomical interest, since looked at broadly it is much more primitive than that of any other Reptile so far described. On the one hand, it has resemblances to the Crocodilia, Chelonia, particularly the Lacertilia, and even the Ophidia, while on the other hand it recalls in a number of striking features that characteristic of the Urodela. In it then we have an arrangement that should be borne in mind when dealing with other forms, and one that is essential to a proper appreciation of the disposition of the vessels in the Lacertilia.

## Conclusions.

As was pointed out in the introduction, two views are commonly held with regard to the systematic position of *Sphenodon*. The more common and perhaps more orthodox view, since it is the one put forward in most text-books, is that *Sphenodon* is the sole modern representative of an order of the Reptilia termed the Rhynchocephalia, equal in rank to the other four orders of the class. This suggestion was first put forward by Günther (41) in 1867. As far as palæontological records show, the order is ancient but was never an extensive one. On this ground there is no inherent improbability in its only remnant being found in Australasia, since this region has

furnished other examples of orders of animals either poorly represented or not represented at all in other parts of the world. The second view put forward by HUXLEY, among others, is that the differences between *Sphenodon* and some of the least specialised Lacertilia are not so great as to justify placing it in a separate order, but, on the contrary, it should be included in the Lacertilia. It is not intended in the present paper to discuss fully all the evidence for and against these two views, but at the same time, in the course of comparing the blood vessels with those of a number of other Reptiles, it was inevitable that some attention had to be paid to evidence put forward by various writers as to the systematic position of the animal.

A full enumeration of the characteristic features of *Sphenodon* and discussions as to their value will be found in the works of BOULENGER (16), BUSCH, GADOW and HOWES and SWINNERTON, and they need not be repeated here. One or two points have been raised subsequently and call for brief notice.

GADOW (29) pointed out that *Sphenodon* lacks distinct copulatory organs, and so is to be regarded as a primitive type, and he even pointed out similarities between the cloaca in this form and in the Gymniophiona. Later, OSAWA (63) sought to homologise the cloacal scent glands with the copulatory organs of other Reptiles, and concludes (p. 346), ". . . muss ich mit der Behauptung auftreten, dass der *Hatteria* auch ein Begattungsorgan zukommt." The impossibility of homologising the scent glands with copulatory organs, for both may occur together in Snakes, was subsequently reaffirmed by GADOW, who concluded (30, p. 43): "*Hatteria* ist und bleibt das niederste lebende Reptil welches wir kennen; es gehört weder zu den Krokodilen, was niemand behaupten wird, noch zu den Saurien, . . ."

Another of these features is the characteristic forward extension of the pterygoid bones to meet the vomers, so that the palatines are, as it were, pushed to the side and excluded from participation in the formation of the middle portion of the bony palate. This, as HOWES and SWINNERTON point out, is "a feature already recognisable among the Batrachia and Stegocephalia." BEDDARD (6) afterwards described the skull of *Uromastix spinipes*, in which the pterygoids pass forwards almost, if not actually, to touch the vomers, and so called attention to the fact that this character, supposed to be peculiar to "Hatteria," is also found in a Lacertilian. This condition is very unusual in the Lacertilia; indeed, it does not appear to be found in any other species that has been described, not even in the closely allied *Uromastix hardwickii*, according to BUSCH (20). It cannot therefore be urged as showing any relationship between *Sphenodon* and the Lacertilia, for it is distinctly atypical of that order, but is better regarded as (so far as known) an isolated example of a species of Lizard that has retained a Batrachian condition that is also found in *Sphenodon* in a more complete form.

We are here more concerned with the blood vascular system than with other anatomical features, and it will simplify matters if we glance briefly at the points that have come to light in comparing *Sphenodon* with other forms. In other

Reptilia the three main arterial trunks come off separately from the ventricle, while in the Tuatara they come off from a short common trunk, probably representing the conus arteriosus of the Amphibia which has been lost in other Reptilia.

*Sphenodon* possesses both a ductus caroticus and a ductus arteriosus (BOTALLI) on each side, and they are in a moderately developed condition. That this is a primitive condition is shown by the fact that it occurs in the Amphibia Urodela, and is not found, so far as is known, in any other reptile. The carotids, in origin and general distribution, and also in the absence of a common trunk, *i.e.*, a carotis primaria, resemble those of the Urodele Amphibia, and also some of the primitive Lacertilia. The same is also true of the arteria laryngeo-trachealis, which comes off from the pulmonary artery in Amphibia and in certain Lizards. This vessel appears to be homologous with the arteria œsophagea of the Urodeles, and so is a relic of the time when respiration took place in the mucous membrane of the buccal cavity and pharynx. VAN BEMMELEN (10, p. 102) gives his opinion of the neck region as follows: "Vor allem stellte es sich heraus, dass *Hatteria*, im Baue ihrer Halsgegend eine typische Eidechse ist, und darin besonders mit den Ascalaboten sehr übereinstimmt." As was noted previously, he was mainly concerned with the nerves. DENDY (22) gives a comparison between the intra-cranial arteries of *Sphenodon* and other reptiles. He notes several points of difference from the Lacertilia, but, nevertheless, records the general impression (p. 411) that "the arrangement of the cerebral arteries in *Sphenodon* strongly supports the view that that animal is closely related to the Lacertilia, though it approaches the more primitive condition of the Chelonia as regards the basilar artery."

In regard to the gut arteries, HOCHSTETTER, in his comparative account of these vessels in Saurians, says (44, p. 217): "Dabei werde ich von *Hatteria* ausgehen, weil bei dieser Form entschieden die ursprünglichsten Verhältnisse bei *Lacerta* von denen bei *Hatteria* in einfacher Weise ableiten lassen." The same conclusion is put forward by GEGENBAUR (33, footnote, p. 536).

The arteria interossea leaves the extensor surface of the fore foot and passes through between the ends of the radius and ulna on to the flexor surface. It returns again, passing through the wrist between the carpal bones. This rather striking course is also primitive, since it is met with in the Amphibia.

Certain points in the relationships of the veins also deserve consideration. The paired venæ tracheales are in a more primitive condition than in *Lacerta*, and, indeed, represent a stage that is actually passed through by *Lacerta* in the course of its development. In all probability they are homologous with the venæ pharyngeæ in Urodele Amphibia. The vena cerebralis posterior in *Sphenodon* leaves the cranium by the foramen jugulare in company with the tenth cranial nerve, a very important point, as this vein is more or less constant in position throughout the vertebrate series. It accompanies the vagus nerve in Elasmobranchs, Urodele and Anurous Amphibia, Birds and Mammals, so that it must be regarded as primitive and

fairly constant. In Lacertilia, and, as far as is known, Ophidia, this vessel leaves the cranium through the foramen magnum, and is thus separated from the vagus. This, then, is a significant difference between *Sphenodon* and the Lacertilia. The vena cerebralis media and the vena capitis dorsalis are both to be regarded as primitive, since they characterise the primitive Amphibia and Reptilia. DENDY (22) has noted several points which, in my opinion, constitute considerable differences between the intra-cranial veins of *Sphenodon* and the Lacertilia, and points out (p. 423) that "a very characteristic feature of *Sphenodon* is the development of large transverse sinuses resembling those of the Crocodile, but these communicate with the extra-cranial vascular system in quite a different manner from that described by RATHKE in the latter animal." There is present a sinus orbito-nasalis, corresponding with a vein of the same name in the Amphibia and Elasmobranchs, and this is not found in *Lacerta* or *Tropidonotus*.

In *Sphenodon* the state of development of the vena azygos and the supra-renal portal system, and also the relations of these vessels, which are remnants of the embryonic posterior cardinal vein, are more primitive than in *Lacerta*, and indeed present a condition from which any of the arrangements met with in the Lacertilia can be derived. The anterior gastric vein resembles that of the Urodele Amphibia, and although present in an Ophidian *Eryx*, does not appear to have been described in Lacertilians. The constitution of the anterior abdominal vein, while resembling that in *Lacerta* to a certain extent, and also the Urodela, is more primitive than in any member of the order to which the former belongs. BEDDARD, as the result of his work on the body veins of *Sphenodon*, concludes (7, p. 462) :—"There is no question that, apart from details, the venous system of *Hatteria* is distinctly Lacertilian. Nor do the differences which it shows from the Lacertilia tend to prove a nearer resemblance to the Chelonia or to the Crocodilia. On the other hand, I believe it possible to detect likenesses to the Ophidia. This, however, in my opinion, does not argue a special affinity between *Hatteria* and the Ophidia, but the antiquity of the *Hatteria* type which Palæontology, as is well known, has proved." Notwithstanding this view of one who has a very extensive knowledge of the blood vessels in the Reptilia, it seems to me that, when a more extended survey is taken and the many points of similarity between the vessels of *Sphenodon* and the Amphibia, especially the Urodela, are borne in mind, the above conclusions hardly go far enough, and that the primitiveness of *Sphenodon* is considerably more pronounced than they appear to indicate.

Thus, I think, it will be seen that in a large number of points, some of considerable importance, the vascular system of the Tuatara is more primitive than that in any of the Lacertilia. Indeed, if we consider the cumulative effect of all these points, it seems inevitable that we must regard the vascular system as a whole as being of a much less specialised type, so much so that it merits the placing of the animal in a separate order. Certain features need re-emphasising, the unspecialised condition of

the heart, the retention of the ductus caroticus and arteriosus, and the position of the posterior cerebral vein. In this last matter, *Sphenodon* resembles both the higher and lower Vertebrates, while the Lacertilia have departed from this condition. Also, there does not appear to be any primitive condition in the vessels of any Lacertilian that is not also found in *Sphenodon*; and yet, again, in its intra-cranial vessels it gives a suggestion of the conditions realised in the Chelonia and the Crocodilia, which is just what might be expected of a primitive form.

The fact that *Sphenodon* resembles the Lacertilia in certain respects, not alone in the blood vessels, as BEDDARD has pointed out, does not, I submit, justify its inclusion in this order any more than its likenesses to the Urodela, which are many, demand its being placed with them. Indeed, the fact that *Sphenodon* has structures to be found in various Lacertilians, but not all in the same species, or even in the same genus, seems to suggest, and rather forcibly too, that when such characters are encountered in one of the Lacertilia it indicates that, in this particular respect, the Lizard has retained a primitive condition which is present in the Tuatara, and that the latter animal is more primitive than any of them. The Lacertilia differ among themselves in the disposition of their blood vessels, but when they do it is the result of modification or specialisation; whereas practically always when *Sphenodon* differs from them it will be found to be in a way that either suggests conditions in other Reptiles or most frequently approximates it more nearly to the Urodela.

The object of the present investigation was in the first place to give a fairly complete account of the blood vascular system of the Tuatara, as, owing to its rarity, an opportunity of examining a well preserved series of specimens might not occur again. Secondly, no such complete account is available for any Lacertilian, and as a large amount of comparative work has been done on various points in different species of Reptiles, it seemed desirable to correlate this with such an admittedly little specialised type to form a basis for future comparative work.

At the outset I was inclined to regard *Sphenodon* as in all probability a lowly member of the order Lacertilia. The condition of its vascular system, briefly epitomised above, however, was found to be so primitive in all respects, and to differ so much from that in the Lacertilia in certain important features, that it was obvious that it could not be included in that order. Reference to the somewhat extensive literature regarding other points in its anatomy disclosed no valid reason that would necessitate its being placed among the Lacertilia; but, on the other hand, it brought out a number of points (more than need be dealt with here) to show it to be a more primitive type of Reptile. I have therefore been led to conclude that while *Sphenodon* approaches the Lacertilia more closely than any other order of the Reptilia, it nevertheless differs from them to such an extent that GÜNTHER was thoroughly justified in placing it in a separate order, the Rhynchocephalia, and that it is the most primitive living Reptile.

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## DESCRIPTION OF PLATES.

### Plate 6.

Fig. 1.—Diagrammatic sketch of a general view of the viscera of Sphenodon, with the alimentary canal displaced to the right.

*Vessels.*

*A.C.*, arteria cœliaca; *A.E.A.*, arteria epigastrica anterior; *A.I.C.*, arteria iliaca communis; *A.Il.E.*, arteria iliaca externa; *A.L.*, arteria lumbalis; *A.M.C.*, arteria mesenterica communis; *A.S.*, arteria scapularis; *C.E.*, carotis externa; *C.I.*, carotis interna; *D.Ao.*, dorsal aorta; *R.E.A.* 1, ramus muscularis of arteria epigastrica; *V.*, ventricle; *V.A.A.*, vena abdominalis anterior; *V.Az.*, vena azygos; *V.C.A.S.*, vena cava anterior sinistra; *V.Co.C.*, vena coraco-clavicularis; *V.C.P.*, vena cava posterior; *V.Cu.L.*, vena cutanea lateralis; *V.Cu.M.*, Vena cutanea magna; *V.Il.*, vena iliaca communis; *V.J.E.*, vena jugularis externa; *V.J.I.*, vena jugularis interna; *V.Pl.*, vena parietalis lateralis; *V.R.R.*, venæ renales revehentes; *V.Sc.*, vena subclavia; *V.Sp.D.*, vena spermatica dextra; *V.Sp.S.*, vena spermatica sinistra; *V.Ve.*, venæ vesicæ.

*Other Structures.*

*Blad.*, bladder; *G.Blad.*, gall bladder; *Int.*, intestine; *Liv.*, liver; *Mesor.*, mesorchium; *Rect.*, rectum; *Rib.*, cut end of ribs; *Rt.Kid.*, right kidney; *Rt.Lung*, right lung; *Rt.Tes.*, right testis.

PLATE 7.

Fig. 2.—Diagrammatic sketch of the vessels shown in a lateral dissection of the head, certain of the bones having been removed.

*Vessels.*

*A.A.*, arteria articularis; *A.Au.*, arteria auricularis; *A.F.*, arteria frontalis; *A.Mn.*, arteria mandibularis; *A.M.G.*, arteria musculo-glandaris; *A.Mn.E.*, arteria mandibularis externa; *A.Mn.I.*, arteria mandibularis interna; *A.N.*, arteria nasalis; *A.Oc.*, arteria occipitalis; *A.O.I.*, arteria orbitalis inferior; *A.Op.*, arteria ophthalmica; *A.O.S.*, arteria orbitalis superior; *A.T.*, arteria temporalis; *R.C.*, ramus coronoideus; *R.C.I.*, 1 and 2, rami musculares of arteria temporalis; *R.Mn.* 1, 2 and 3, rami musculares of arteria mandibularis; *R.m.n.*, ramus membranæ nictitantis; *R.t.m.*, ramus temporo-masseteris; *S.M.N.*, sinus membranæ nictitans; *S.O.*, sinus orbitalis; *V.Ce.L.*, vena capitis lateralis; *V.Ce.M.*, vena cerebralis media; *V.Ce.P.*, vena cerebralis posterior; *V.Ce.R.*, ramus muscularis of vena cerebralis posterior; *V.J.I.*, vena jugularis interna; *V.J.R.* 2–6, rami musculares of vena jugularis interna; *V.Mn.*, vena mandibularis; *V.Mn.I.*, vena mandibularis interna; *V.Mn.R.*, rami musculares of vena mandibularis; *V.Oc.*, vena occipitalis; *V.Pt.*, vena pterygoidea; *V.S.*, vena supra-temporalis; *V.T.A.*, vena tympanica anterior; *V.T.A.R.*, ramus muscularis of vena tympanica anterior.

*Other Structures.*

1, cleido-humeralis muscle; 2, ventral part of levator scapulæ; 3, dorsal part of levator scapulæ; 4, longissimus; 5, cucullaris; 6, cut end of parietal bone; 7, parietal bone; 8, columella cranii; 9, cut end of post-frontal bone; 10, rectus superior; 11, frontal bone; 12, obliquus superior; 13, Harderian gland; 14, obliquus inferior; 15, rectus inferior; 16, cut end of jugal bone; 17, coronoid process of mandible; 18, cut end of quadrato-jugal bone; 19, cut end of squamosal and quadrate bones; 20, anterior hyoid bone; 21, posterior hyoid bone; *V*, nervus trigeminus; *X*, vagus.

Fig. 3.—Diagrammatic sketch of the arteries and veins shown in a dissection of the head and neck from the ventral side.

*Vessels.*

*A.Gg.*, arteria genio-glossa; *A.Gp.*, arteria glossopharyngeus; *A.L.T.*, arteria laryngeo-trachealis; *A.M.*, arteria muscularis cervicis; *A.Oe.*, arteria œsophagea; *A.P.S.*, arteria pterygoideus superficialis; *A.S.M.*, arteria submandibularis; *A.T.I.*, arteria thyreoidea inferior; *A.T.S.*, arteria thyreoidea superior; *C.C.*, carotis communis; *C.E.*, carotis externa; *C.I.*, carotis interna; *D.C.*, ductus caroticus; *L.S.A.*, left systemic arch; *R.m.m.*, ramus musculo-mandibularis; *S.A.*, systemic arch; *V.C.A.D.*, vena cava anterior dextra; *V.J.C.D.*, vena jugularis communis dextra; *V.J.C.S.*, vena jugularis communis sinistra; *V.J.E.*, vena jugularis externa; *V.J.I.*, vena jugularis interna; *V.J.R.* 1–5, rami musculares of vena jugulares; *V.O.*, venæ œsophageæ; *V.Sc.*, vena subclavia; *V.T.R.I.*, ramus muscularis of vena trachealis.

*Other Structures.*

*Cer.Sym.*, cervical sympathetic; *Gen.gl.*, genio-glossus; *Gen.hy.*, genio-hyoid; *Hy.* 1, anterior cornu of hyoid; *Hy.* 2, posterior cornu of hyoid; *Hyo-man.*, hyo-mandibularis; *Int.Pte.*, internal pterygoid; *Lev.Hy.*, levator hyoidens; *Plat.*, platysma; *Rec.Lar.X.*, recurrent laryngeal of vagus; *Tra.*, trachea; X., vagus; XII., hypoglossal.

PLATE 8.

Figs. 4–10, Diagrammatic Sketches—

Fig. 4.—Vessels of the left hind limb viewed from the extensor surface.

Fig. 5.—Deeper arteries of the right hind foot viewed from the flexor (plantar) side.

Fig. 6.—Veins of the right hind limb viewed from the extensor surface.

Fig. 7.—Veins of the right fore limb viewed from the extensor surface.

Fig. 8.—Vessels of the left fore limb viewed from the extensor surface.

Fig. 9.—Vessels of the left fore limb viewed from the flexor surface.

Fig. 10.—Relation of the arteries to the muscles of the eye viewed from the inner aspect.

*Muscles of Hind Limb.*

5, ileo-femoralis; 9, ischio-trochantericus; 11, ischio-tibialis posticus; 13, ilio-fibularis; 14, extensor triceps; 15, gastrocnemius; 16, flexor digitorum communis profundus; 17 and 20, tibialis anticus; 21, extensor digitorum communis longus; 22, peroneus; 23, abductor et extensor hallucis longus; 29, abductor digitorum communis; 32, interossei planteres.

*Arteries of Hind Limb.*

*A.C.F.E.*, arteria circumflexa femoris externa; *A.C.F.I.*, arteria circumflexa femoris interna; *A.C.G.E.*, arteria circumflexa genu externa; *A.C.G.I.*, arteria circumflexa genu interna; *A.D.P.*, arteria dorsalis pedis; *A.I.*, arteriæ interdigitales; *A.I.E.*, arteria interossea externa; *A.Io.*, arteria interossea; *A.Is.*, arteria ischiadica; *A.M.E.*, arteria metatarsalis externa; *A.M.I.*, arteria metatarsalis interna; *A.P.P.*, arteria perforans plantaris; *A.T.L.*, arteria tibialis lateralis; *A.T.M.*, arteria tibialis media; *R.I.C.* 1 and 2, rami musculares 1 and 2 of the arteria iliaca communis.

*Veins of Hind Limb.*

*V.A.V.*, vena anastomotica arcus venosi; *V.C.G.*, vena circumflexa genu lateralis inferior; *V.C.T.*, vena circumflexa tarsi; *V.Cu.* 1 and 2, venæ cutaneæ; *V.D.P.*, vena dorsalis pedis; *V.D.R.* 5, ramus muscularis of the vena dorsalis pedis; *V.F.*, vena femoralis; *V.F.R.* 1 and 2, rami musculares of the vena femoralis; *V.I.*, venæ interdigitales; *V.Pe.*, vena peronea; *V.Po.*, vena poplitea; *V.Po.R.* 4, ramus muscularis of the vena poplitea; *V.P.P.*, vena præ-pollicis.

I Pollex; II–V digits (figs. 4–6).

*Muscles of Fore Limb.*

2, latissimus dorsi; 11, pectoralis; 12, cleido-humeralis; 13, dorsalis scapulæ; 14, supra-coracoideus; 15, coraco-brachialis; 17, scapulo-humeralis posterior; 18, scapulo-coraco-brachialis; 19, coraco-antibrachialis; 22, anconæus; 23, flexor-carpi-radialis; 24, flexor-digitorum-communis-profundus; 26, pronator teres; 27, pronator quadratus; 28, supinator; 29, extensor carpi radialis brevis; 30, extensor digitorum communis longus; 31, extensor carpi ulnaris; 32, anconæus quartus (richtiger quintus); 33, extensor carpi radialis longus; 34, abductor et extensor pollicis longus; 35, flexor digitorum communis sublimis; 43, extensor digitorum communis brevis.

*Arteries of Fore Limb.*

*A.B.*, arteria bicipitalis; *A.I.*, arteriæ interdigitales; *A.I.E.*, arteria interossia externa; *A.Io.*, arteria interossea; *A.U.*, arteria ulnaris; *A.V.*, arteria volaris; *A.V.P.*, arcus volaris profundus; *R.r.*, ramus radialis; *Rr.* 1, ramus radialis of arcus dorsalis; *Ru.*, ramus ulnaris; *Ru.* 1, ramus ulnaris of arcus dorsalis.

*Veins of Fore Limb.*

*A.V.D.*, arcus venosus dorsi manus; *V.A.L.*, vena anastomatica longa; *V.A.S.*, vena antibrachialis superficialis; *V.A.V.*, vena anastomatica arcus venosi; *V.B.*, vena branchialis; *V.B.R.*, *V.B.R.* 2, rami musculares of vena brachialis; *V.Cu.M.*, vena cutanea magna; *V.I.*, vena interdigitales; *V.Io.*, vena interossea; *V.P.B.*, vena profunda brachii; *V.P.H.*, vena præ-hallucis.

Sketch of Dissection of Eye from inner aspect (fig. 10).

*Arteries.*

*A.F.*, arteria frontalis; *A.M.G.*, arteria musculo-glandaris; *A.N.*, arteria nasalis; *A.Op.*, arteria ophthalmica; *A.O.S.*, Arteria orbitalis superior; *C.* 1, branch to posterior rectus; *C.* 3, branch to superior rectus; *C.* 4, branch to back of eye; *C.* 5, branch to anterior rectus; *C.* 6, branch to inferior rectus.

*Muscles.*

*Rect.Ant.*, rectus anterior; *Rect.Inf.*, rectus inferior; *Rect.Post.*, rectus posterior; *Rect.Sup.*, rectus superior; *Ret.Bul.*, retractor bulbi; *Obl.Inf.*, obliquus inferior; *Obl.Sup.*, obliquus superior; *Hard.Gl.*, Harderian gland; *II.*, optic nerve.

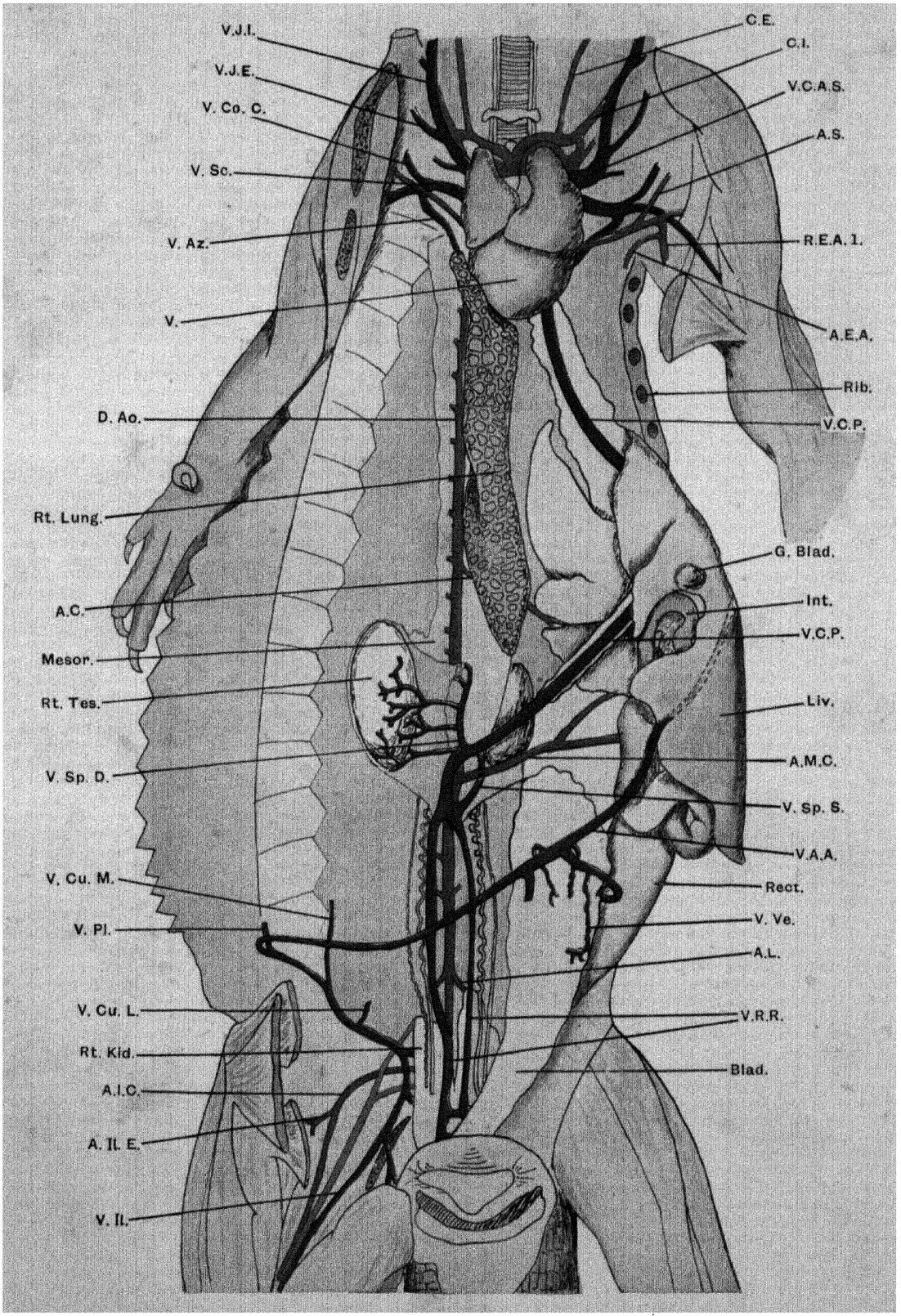

V.J.I.
V.J.E.
V. Co. C.
V. Sc.
V. Az.
V.
D. Ao.
Rt. Lung.
A.C.
Mesor.
Rt. Tes.
V. Sp. D.
V. Cu. M.
V. Pl.
V. Cu. L.
Rt. Kid.
A.I.C.
A. Il. E.
V. Il.
C.E.
C.I.
V.C.A.S.
A.S.
R.E.A. I.
A.E.A.
Rib.
V.C.P.
G. Blad.
Int.
V.C.P.
Liv.
A.M.C.
V. Sp. S.
V.A.A.
Rect.
V. Ve.
A.L.
V.R.R.
Blad.

FIG. 1.

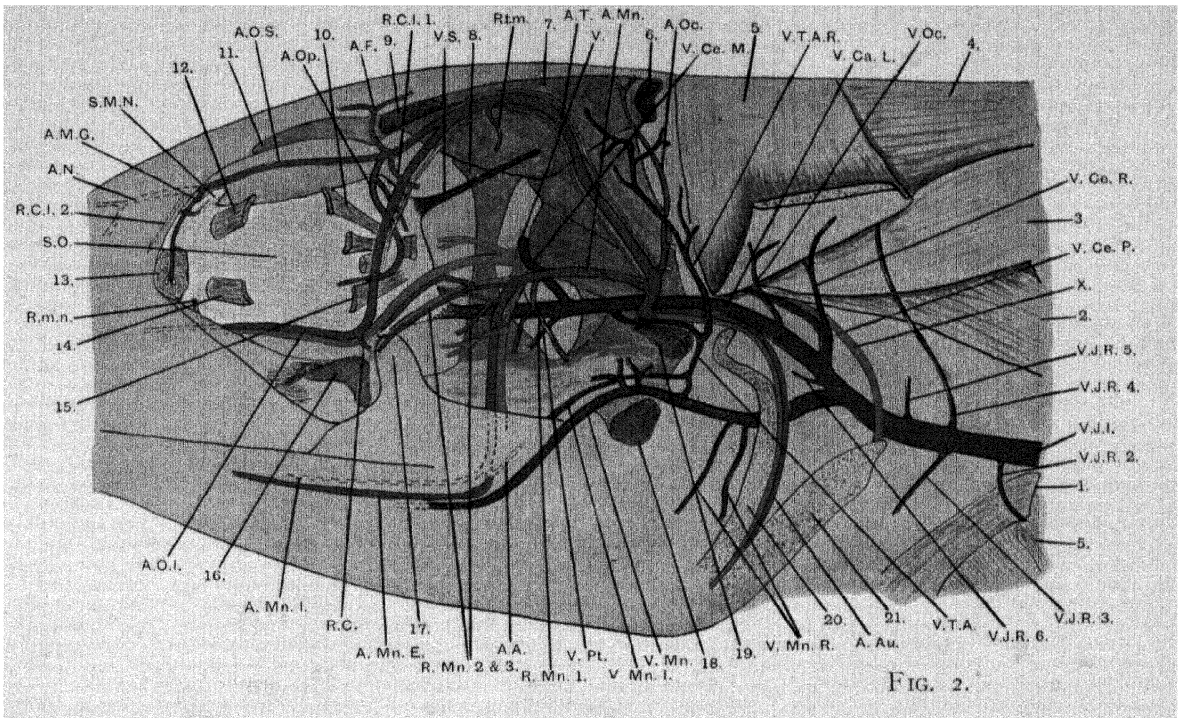

A.O.S.
10.
R.C.I. 1.
Rtm.
7.
A.T.
A.Mn.
A.Oc.
5
V.T.A.R.
V.Oc.
4.
11.
A.Op.
A.F.
9.
V.S. 8.
V.
6.
V. Ce. M.
V. Ca. L.
12.
S.M.N.
A.M.C.
A.N.
R.C.I. 2.
S.O.
13.
R.m.n.
14.
15.
V. Ce. R.
3.
V. Ce. P.
X.
2.
V.J.R. 5.
V.J.R. 4.
V.J.I.
V.J.R. 2.
1.
5.
A.O.I.
16.
A. Mn. I.
R.C.
17.
A. Mn. E.
R. Mn. 2 & 3.
A.A.
R. Mn. 1.
V. Pt.
V. Mn. I.
V. Mn. 18.
19.
V. Mn. R.
20.
A. Au.
21.
V.T.A.
V.J.R. 6.
V.J.R. 3.

FIG. 2.

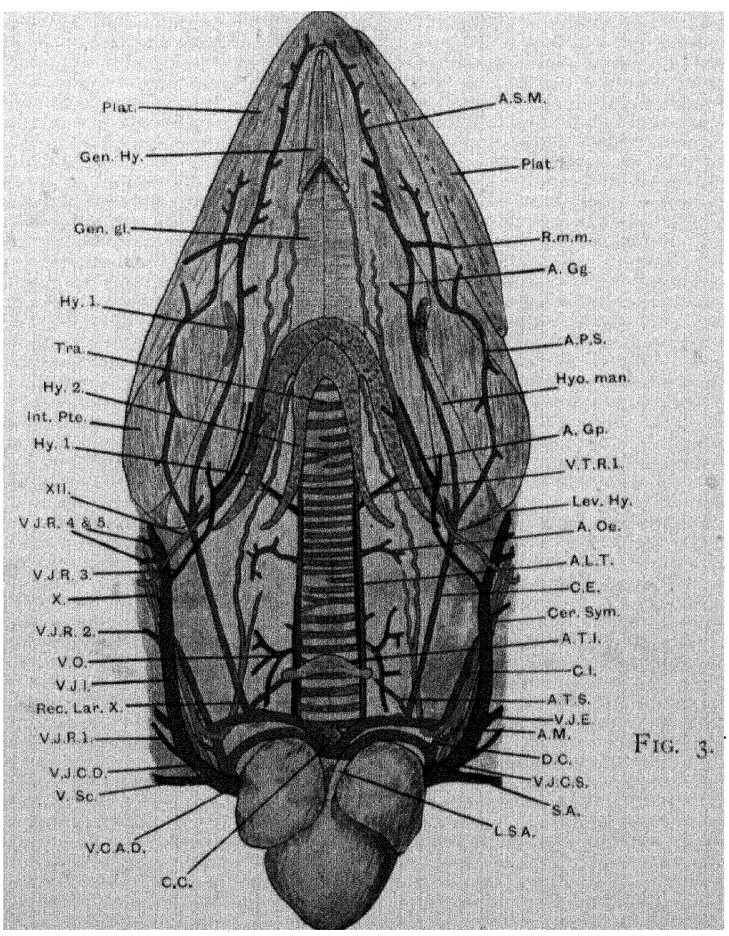

Plar.
A.S.M.
Gen. Hy.
Plat.
Gen. gl.
R.m.m.
A. Gg.
Hy. 1.
A.P.S.
Tra.
Hyo. man.
Hy. 2.
Int. Pte.
A. Gp.
Hy. 1.
V.T.R.1.
XII.
Lev. Hy.
V.J.R. 4 & 5.
A. Oe.
V.J.R. 3.
A.L.T.
X.
C.E.
Cer. Sym.
V.J.R. 2.
A.T.I.
V.O.
C.I.
V.J.I.
A.T.S.
Rec. Lar. X.
V.J.E.
V.J.R.1.
A.M.
D.C.
V.J.C.D.
V.J.C.S.
V. Sc.
S.A.
L.S.A.
V.C.A.D.
C.C.

FIG. 3.

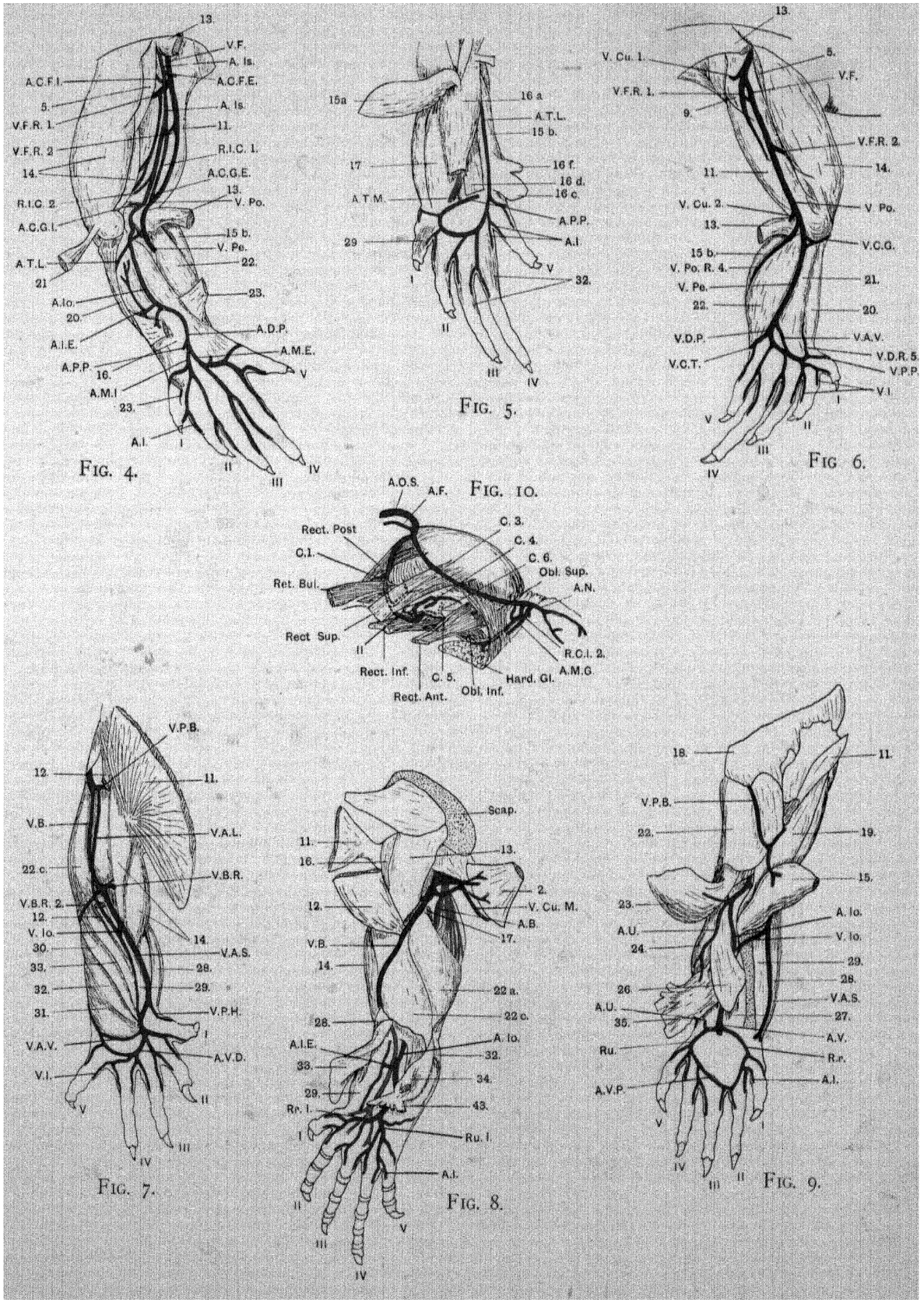



FIG. 4.

FIG. 5.

FIG. 6.

FIG. 10.

FIG. 7.

FIG. 8.

FIG. 9.

# VII.—*On the Structure and Affinities of* Acmopyle Pancheri, Pilger *

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(*Communicated by Prof.* A. C. Seward, *F.R.S.*)

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[Plates 9–11.]

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## Introductory.

Our knowledge of the monotypic New Caledonian genus *Acmopyle* is practically confined to incomplete descriptions of the external features by A. Brongniart and Gris (1869), Sir J. D. Hooker (1902), and Pilger (1903). The only other accounts of the plant are brief references in the 'Genera Plantarum' (Bentham and Hooker, 1883), the 'Kew Bulletin' (1892), and 'The Gardeners' Chronicle' (Masters, 1892). I therefore gladly welcomed Prof. Seward's suggestion that I should undertake an investigation of some material collected in New Caledonia by Prof. R. H. Compton, M.A., during his expedition to that island in 1914.† My very sincere

* Thesis approved for the degree of Doctor of Science at the University of London, 1919.

† A preliminary account of this work was read before the Cambridge Philosophical Society on May 20, 1918. See 'Nature,' vol. 101, p. 299.

thanks are due to Prof. COMPTON for his generosity in allowing me to work at this rare material.

To Prof. SEWARD I owe a debt which I cannot adequately express; besides affording me the opportunity for carrying out this research, he showed an unfailing and kindly interest in the work, which, with his advice and able criticism on difficult theoretical questions, was quite indispensable to me. I am also deeply grateful to him for the privilege of consulting the proofs of the fourth volume of his work on Fossil Plants, the publication of which is shortly expected.

New Caledonia shares with many other islands in the Pacific the possession of a large number of endemic species. So far as the Podocarpineæ are concerned, PILGER (1903, p. 36) has already drawn attention to the peculiarities of the New Caledonian flora, which includes at least nine species of Podocarpineæ hitherto recorded only from that island. With the exception of *Acmopyle*, all of these plants are being investigated by Mr. C. P. DUTT, of Queen's College, Cambridge. Mr. DUTT was kind enough to allow me to examine his preparations for comparison—a fact which helped me considerably in my work on *Acmopyle*. In particular, I would like to thank him for allowing me to reproduce in this paper a photograph (Plate 11, fig. 31), of the stone of a new species of *Podocarpus* discovered by Prof. COMPTON in New Caledonia.

The material of *Acmopyle* was originally preserved mostly in formalin, but was subsequently transferred to a mixture of alcohol and glycerine. It consisted of vegetative shoots bearing twigs with pectinately arranged leaves; a stouter piece of stem with about twenty well marked growth rings; male cones in two stages of development; and over a dozen megastrobili. At the time of collection, March 10, 1914, the ovules had all reached the stage when they contain young embryos at the ends of the tortuous suspensor tubes; they had evidently received the last year's pollen. The fact that most of the male cones collected were nearly mature, suggested that younger ovules (in a stage shortly before pollination) would also be present, but there were none such in the material at my disposal. It is hoped that this unfortunate gap will soon be filled up when more material becomes available.

Through the courtesy of the Director I obtained from the Royal Botanic Gardens, Kew, some material of roots and leaves from two young plants growing in the Temperate House. I would also like to thank Mr. L. A. BOODLE for facilities to fix this material at the Jodrell Laboratory.

Besides the two young plants at the Kew Gardens there is another at the Glasnevin Garden, Dublin, from which, through the great kindness of the Director, Sir F. MOORE, I received a fresh twig which has been very useful for comparison.

This research was aided by a Research Studentship at Emmanuel College, Cambridge, and by a grant from the Dixon Fund of the University of London. To both these bodies I am thankful for the financial help.

## Historical.

In 1869 A. Brongniart and Gris described under the name *Dacrydium Pancheri* some specimens collected in New Caledonia and sent to them by Pancher. In the notes attached to his specimens the latter had named the plant *Podocarpus pectinata*, a designation which apparently still persists in nurseries. Whereas this name is fully justified by the *Podocarpus*-like habit, and by the form and arrangement of the largest leaves, which are quite distinct from those commonly associated with *Dacrydium*, the position of the micropyle led Brongniart and Gris to transfer the plant to the latter genus. Here it was supposed to occupy a peculiar position, firstly, on account of the drupaceous character of the seed—another feature that justifies Pancher's reference to *Podocarpus*—and, secondly, because of the entire absence, as the joint authors believed, of the structure now generally known as the epimatium. The brief account by Brongniart and Gris, based only on vegetative material and immature seeds, was unaccompanied by figures.

In 1902 Sir J. D. Hooker published, for the first time, figures of a shoot bearing male cones, and of stamens showing the dehiscence of the pollen-sacs. Following the Genera Plantarum he placed the plant in the genus *Podocarpus* (§ Dacrycarpus). Hooker, though unable, in the absence of female flowers and ripe fruit, to fix the generic position of the plant, suggested the possibility that it might prove to be an independent genus.

In 1903 Pilger transferred the plant to a new genus of doubtful affinity, and called it *Acmopyle Pancheri*, the generic name having reference to the position of the micropyle, which, however, is not strictly apical. He was the first to describe the ripe seed, in which the micropyle is according to him hardly visible. In the absence of young ovules he leaves undecided the question as to the existence of an epimatium and, with it, the problem as to whether the entire thickness of the seed-coat is formed by the integument alone. His description is on the whole correct, but the biseriate disposition of the leaves on the terminal shoots, although mentioned in the text, does not appear in the figure. In his dried material, moreover, Pilger appears to have missed the curved ridge at the back of the seed.

Coulter and Chamberlain (1917, p. 353) have recently referred *Acmopyle** to the Taxineæ, thus placing it nearer to *Taxus* than to *Podocarpus*. This is evidently due to oversight, for the little that is known about the plant points clearly to an affinity with *Podocarpus* rather than with *Taxus*.

In the published literature the plant is first mentioned as having been introduced into England in 1891, when the Royal Gardens at Kew ('Kew Bulletin,' p. 105) received a living specimen from the Sydney Botanic Garden. This plant flowered at Kew in 1902, only male flowers being produced, so far as I can ascertain; it is the original of Hooker's figures (1902), the first ever published. Masters (1892) also

* And also *Polypodiopsis*, which has long been known as a synonym of *Podocarpus vitiensis*, A. Brongn. See Bertrand, 1874, p. 65.

drew attention to a plant having been discovered at the Orchid Nurseries of Messrs. Sanders, of St. Albans, England.

## Descriptive.

### A. *Distribution and Habit.*

Pilger mentions *Acmopyle* as being peculiar to New Caledonia. There is, however, at the Royal Herbarium, Kew, a specimen which although unfortunately sterile, in its vegetative features, external and internal, agrees so closely with *Acmopyle* that it is undoubtedly to be referred to this genus.* The specimen is labelled :

"Fiji Islands. Coll. J. Horne, 1877–78. Received March, 1879,"

but Horne in his book "A Year in Fiji" (1881) does not mention it, possibly because he had no flowers. On the other hand it is, of course, possible that there was an error in labelling the specimen as coming from Fiji. But considering that *Podocarpus elata* R. Br. remained unnoticed in Fiji till 1907 when it was first recorded by Miss L. S. Gibbs† (1909, p. 183) it would not be astonishing if in the absence of flowers *Acmopyle* has escaped detection.

The photograph on Plate 9, fig. 1, is from the older of the two plants at the Royal Gardens at Kew, and was taken with the kind permission of the Assistant Director, Mr. A. W. Hill. Although this plant is only a few feet high, while the tree in its native habitat is said to attain a height of 17–20 metres, it gives some idea of the rather yew-like habit of the dorsi-ventral terminal shoots, with their leaves arranged like the pinnæ of a pectinate leaf—a feature which no doubt suggested the specific name adopted by Pancher. There is a wide variation in the number of leaves on each side of these shoots, and local departures from the pectinate arrangement are frequent; this is especially the case in the shoots bearing the male cones, at least so far as can be judged from the available material. Possibly the male shoots are more often held erect, although this is not the impression given by Hooker's figure (1902).

### B. *Root.*

The roots of the Podocarpineæ (except *Pherosphæra* and *Acmopyle*) have formed the subject of a recent paper by Miss Spratt (1913). My material, as already stated, was from the plants growing at Kew, and consisted of young roots up to about 2 mm. thick, with hardly any secondary xylem. As expected, tubercles were present, though only in small numbers. None of them appreciably exceeded the roots in

* I wish to express here my appreciation of Dr. Stapf's kindness in sending me a portion of this specimen, which enabled me to examine it anatomically, and also to thank him for advice concerning the identity of the specimen in question. Dr. Stapf, who kindly examined my sections, does not consider it likely that the Fiji specimen is specifically identical with *Acmopyle Pancheri*, but he agrees to the generic identity.

† I am also much indebted to this lady, who has an intimate knowledge of the flora of Fiji, for her kind advice on the above question.

diameter; several of them had proliferated, having continued their growth distally into normal rootlets (Plate 9, fig. 2), a fact which supports VAN TIEGHEM's view (1869, p. 352) that the tubercles are modified rootlets. In some material collected at a later date no tubercles were present; this may be due to all the tubercles having grown out into normal rootlets.

The stele of the tubercle, like that of the root, is diarch, and lies in the same plane, at least at its point of origin. Root-hairs were altogether absent in my material, both on the root and tubercles.

In the root the cells of the inner cortex show pronounced local thickenings which, in the form of hoops, girdle the cells in different planes. Similar thickenings have been described by NOELLE (1910) in the Araucarineæ, Taxodineæ and Cupressineæ. In section (Plate 9, fig. 3) these thickenings appear like beads, and turn yellow in SCHULTZE's solution. EICHLER (1889, p. 34) also describes delicate spiral thickenings in the outer cortical cells in the roots of *Sequoia gigantea*, *Cryptomeria*, *Chamæcyparis*, and in *Podocarpus*, *Phyllocladus* and *Torreya*. The endodermis consists of 2–3 layers of tabular cells which are in radial seriation and give a bright yellow reaction with SCHULTZE's solution; the outer tangential walls of the outermost layer are much thickened and dark brown. The pericycle, 5–6 layers thick at the sides of the xylem-plate, thins down to 2–3 layers opposite the protoxylems.

The structure of the tubercles presents few features not already noticed by Miss SPRATT in *Podocarpus*. The infected cells lie in an ill-defined zone about halfway out in the cortex (Plate 9, fig. 2); the bars of thickening in the cortical cells are very inconspicuous and sometimes hardly visible, probably because of the young stage of the material.

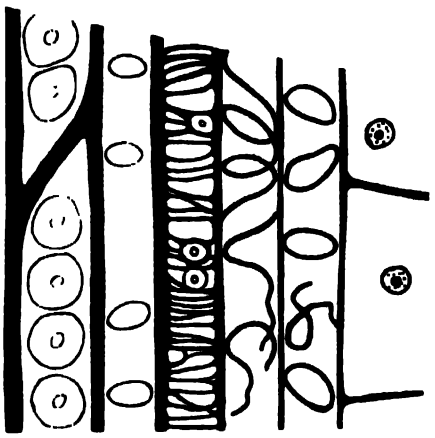
### C. *Stem.*

The stem anatomy closely resembles that well known in *Podocarpus*. A section across a young twig before secondary growth shows the usual ring of collateral endarch strands, each with a mucilage canal outside it.* At this stage the pith and cortex cells are all thin-walled, some of them filled with a homogeneous, brown, resinous-looking substance.† In branches a few years old stone-cells appear in the pith and cortex, while the colourless thin-walled cells become starch-laden. In the oldest shoot available (with about twenty growth-rings in the wood), the secondary phloem contains much-elongated fibres which in transverse section are rectangular; they appear exactly like the flattened "autumn" tracheides, and conform to the radial seriation of the xylem and phloem elements. These fibres are comparable

* The contents of these canals become white and opaque in strong alcohol, are slow in taking up stains, show a finely granular or alveolar structure, and usually include deep-staining tabular crystals of different sizes, varying in shape between triangles, squares and hexagons. See fig. 10, Plate 10.

† Although this substance, so commonly present in the Podocarpineæ and other Conifers, usually passes for resin, it is not soluble in alcohol. The only justification for the use of the word resin is convenience of description.

with the sclerites described by Tison (1909, p. 140) in the secondary phloem of *Saxegothæa*. The secondary phloem also contains abundant "resin"-cells, which are arranged in discontinuous rings concentric with the woody cylinder.



Text-fig. 1.

The secondary wood is so similar to that of *Podocarpus* that it is needless to describe it, but attention must be drawn to the sculpturing of the tracheides composing the protoxylem and the metaxylem adjacent to it. Although the narrower protoxylem elements are of the ordinary spiral or annular type, many of the wider ones are scalariform, and also possess circular or oval pits with or without a border, thus closely resembling the transfusion tracheides in the leaf (see below). Some of the earlier-formed metaxylem elements, even in regions not in contact with medullary rays, show large uniseriate borderless pits (Eiporen) at long intervals, instead of the usual bordered pits (text-fig. 1). Exactly the same type of pitting is seen also in the early metaxylem of the leaf-strand.

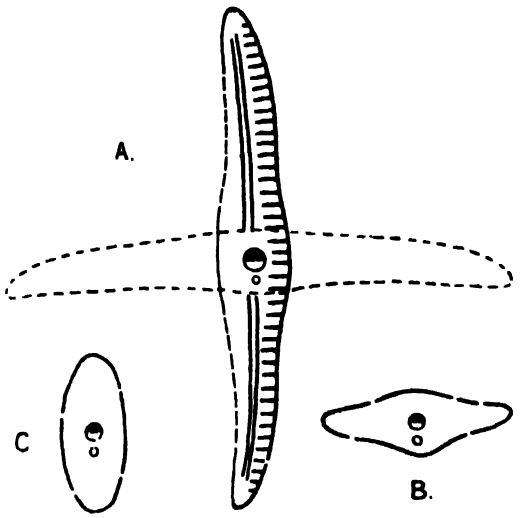
## D. *Leaf.*

The polymorphism of the leaf in the Conifers has for a long time drawn the attention of botanists (Masters, 1891). In *Acmopyle* at least six types of leaves occur in different regions of the plant :—

1. The large triangular scale-leaves on the thicker branches.
2. The minute imbricate scales on the peduncles of the megastrobili.
3. The chief assimilating leaves, further described below.
4. Small laterally compressed leaves with an isobilateral structure, forming the transitions from 1 to 3 and 3 to 2.
5. The sterile bracts on the fleshy receptacle.
6. The fertile bracts.

The leaves on the dorsi-ventral pectinate shoots deserve special mention, for they afford a striking illustration of the direct influence of the orientation of an organ upon its internal structure. The rather fleshy, linear, obtusely pointed leaves have their smooth and shining, slightly convex, upper surfaces directed towards the light (Plate 11, fig. 22*b*), while the shaded under sides present, on each side of the faint midrib, a broad glaucous band to which the stomata are usually confined, but which is not wide enough to extend to the leaf-edge. A transverse section shows a rather unexpected feature : the plane passing through the xylem, phloem, and the associated mucilage canal, instead of being perpendicular to the leaf surface as in all ordinary leaves, is here parallel to it (Plate 9, fig. 4, and text-fig. 2).

Since there is no sign of a torsion in the decurrent leaf-base it is obvious that the leaf is expanded in the antero-posterior plane, so that the middle lines of the actual upper and lower surfaces represent the margins of an ordinary leaf. The whole anatomy of the leaf, except the vascular strand, has, so to speak, been shifted through an angle of 90°. It is clear, also, that this shifting has taken place in opposite directions in the leaves respectively on the right and left sides of the shoot, for the palisade layer is on the morphologically left side in the right-hand series of leaves, and on the morphologically right side in the left-hand series. As BERNARD (1904, p. 256) points out, leaves thus constituted contradict LIGNIER'S view that the accessory transfusion tissue is the remnant of a former system of veins.




TEXT-FIG. 2.—Diagrams to show the organisation of three different types of leaves in *Acmopyle*. In A the palisade tissue is indicated as short transverse lines, and the accessory transfusion tissue as long parallel lines; the broken line shows the position of the lamina in an ordinary leaf (expanded in the horizontal plane). *Xylem*, black; *phloem*, unshaded.

Towards the base and apex of the pectinate shoot, but especially in the latter region, are frequently seen a few smaller leaves, which indicate the manner in which this peculiar structure has been attained. They show all transitions, both in orientation and anatomical structure, between the linear leaves already described and the spirally placed scale-leaves by which they are distally succeeded. Text-fig. 2, C, shows the lenticular transverse section of one of these transitional leaves, expanded in the radial plane, devoid of palisade cells, and with the stomata evenly distributed on the two faces. Leaves expanded in the radial plane, and having an isobilateral structure, are also met with in the New Caledonian species *Dacrydium taxoides*, and probably in several other Podocarpineæ (see MAHLERT, 1885, p. 279, and VAN TIEGHEM, 1891, pp. 169, 171).

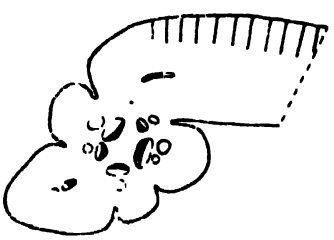
It is well known that, in the horizontal shoots of *Taxus* and many other plants, the apparently distichous arrangement of the leaves is brought about by a torsion in the leaf-bases, some of which at the same time bend round the axis of the shoot, so as to occupy approximately the same (horizontal) plane as the leaves arising from the right and left sides of the axis. In *Acmopyle*, however, no trace of a torsion is seen in any of the leaves; these are all attached by a narrow longitudinally extended base from which the lower edge of the leaf can be followed a considerable distance backwards as a straight decurrent ridge. That here, as in *Taxus*, the leaves arise spirally is seen from the leaf-traces and from the salients caused by the decurrent bases in the outline of a transverse section of the shoot. Since, however, the leaves

are already expanded in the radial plane, a simple bending (unaccompanied by torsion) suffices to bring them into the horizontal position (text-fig. 3), and even this bending is dispensed with in the case of the leaves arising from the sides of the axis.

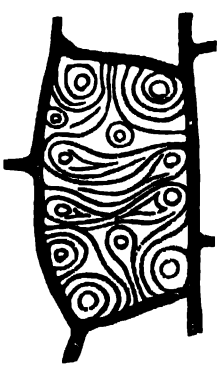
Examples of leaves which show the closest resemblance in principle to those of *Acmopyle* also occur in *Podocarpus imbricatus* Bl. and *P. dacrydioides* A. Rich., a fact noticed in a passing reference by BERNARD (1904, p. 256), but not elucidated by figures.

Prof. GOEBEL has recently (1913, pp. 238–247, 289) described rather similar adaptations in other Conifers (*Thujopsis*, etc.) and some Vascular Cryptogams (*Lycopodium complanatum*, *L. volubile*, *Tmesipteris*). See also BOODLE (1900).

Plate 9, figs. 4–7, and text-fig. 4, illustrate the minute structure of one of the leaves on the pectinate shoot of *Acmopyle*. The thick upper and lower cuticles, the sunken stomata, and the fleshy character of the leaf, are features consistent with the xerophytic habitat of *Acmopyle*. The plant grows, according to PILGER, in rocky places in the south of New Caledonia.* There is the usual palisade layer on the upper side, and the spongy parenchyma below. Sections cut parallel to the leaf surface present a mosaic of large thin-walled mucilage cells, which probably store water, and are responsible for the fleshy nature of the leaf, and groups of much smaller dark-staining palisade cells with abundant interspaces (Plate 9, fig. 5). Hypodermal fibrous elements occur in small numbers on both faces of the leaf, but are confined to the region of the midrib. Between the two mesophylls lies a loose network of transversely elongated cells (Plate 9, fig. 6), several layers thick, extending in the horizontal plane from the median vein to either edge of the leaf. This network consists of (1) thin-walled cells with living contents; (2) dead cells with thick, simply pitted walls ("accessory transfusion tissue," WORSDELL).



TEXT-FIG. 3.



TEXT-FIG. 4.

The transfusion tissue proper, which is as a rule clearly separated from the accessory by a layer or two of parenchyma, is further distinguished by its elements

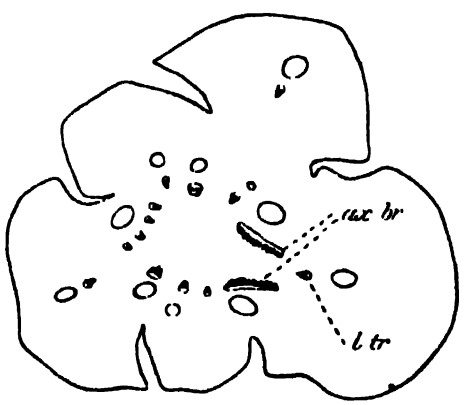
* I have to thank Prof. COMPTON for the following additional information regarding the habitat of *Acmopyle*. The typical situation in which *Acmopyle* grows is in mixed forest containing many species of conifers, on serpentine rocks above 3000 feet altitude. Here it is associated with *Podocarpus minor*, *P. sp.* (unpublished), *Dacrydium taxoides*, *D. lycopodioides*, etc. The majority of arboreal plants in this association show some xerophilous features.

having all their walls provided with crowded bar thickenings, as well as small borderless or narrowly-bordered pits (text-fig. 4). These transfusion tracheides are of two types, one long and narrow, the other considerably broader and nearly isodiametric, but intermediate shapes are also met with. The sculpturing on all is of the same type. The narrower elements are almost all on the side nearest to the protoxylem. In the median plane the transfusion tissue is also separated from the protoxylem by one or two layers of parenchyma, but, laterally, it is often contiguous with the wood. The protoxylem and centrifugal xylem of the leaf show the same types of pitting as described above for the corresponding tissues in the stem.

The epidermal cells, which in the non-stomatiferous regions are longitudinally extended, have straight (as opposed to sinuous) walls, which show moniliform thickenings (Plate 9, fig. 7). The lumina are almost completely filled up by a homogeneous dark brown substance, but the nucleus invariably lies in a pocket in the latter. The stomata are of the usual Gymnospermous type, and the figures on Plate 9, figs. 7*a d*, will suffice to describe them.

### E. *The Vascular Supply of the Axillary Branch*

For reasons stated below, attention is particularly directed to the vascular supply to the axillary branch, which originates as two strands (*ax.br.*), one from each side of the gap in the main cylinder, caused by the subtending leaf-trace (*l.tr.*), (text-fig. 5). Before passing into the branch, the strands turn round, so as to face each other by their xylem ends. It may also be mentioned that this mode of origin is of wide occurrence among Conifers (GEYLER, 1867; STRASBURGER, 1872).




TEXT-FIG. 5.

### F. *Microstrobilus.*

The male cones are terminal, and either solitary, or more frequently in groups of 2–5 or 6 (Plate 10, fig. 12), on short peduncles covered with scales. When in a group they are borne on a branched system of peduncles. Each sporophyll bears two spherical abaxial pollen-sacs, except at the base of the cone, where sporophylls with one and three sacs are of frequent occurrence. The longitudinal section given in Plate 9, fig. 8, shows at × the organic apex of the axis, and at ✱ the terminal sporophyll, which is distinctly peltate. The development of all the sporangia in the cone appears to take place almost simultaneously. Neither in the structure of the cone-axis, nor in that of the sporophylls, is there any important difference from *Podocarpus*; a reference to the figures, and the explanations attached to them, will suffice (Plates 9, 10, figs. 8–12).

As in *Podocarpus* and *Dacrydium*, the pollen-grains have two wings, with reticulate markings (Plate 10, fig. 11). Unfortunately, the contents of the pollen-grains are badly shrunken in all the material, so that the structure of the male gametophyte cannot be definitely ascertained. Not more than one nucleus can with certainty be made out in each pollen-grain, but it is highly improbable that no more are produced.

Another feature, perhaps of little significance, in which *Acmopyle* resembles *Podocarpus*, is the thick-walled character of the pollen-tube (STILES, 1912, p. 483, *P. macrophyllus*).

### G. *Megastrobilus.*

The field notes accompanying the material are not explicit as to whether *Acmopyle* is monœcious or dicœcious, but the probability is in favour of the latter, for none of the published accounts or figures show both sexes as being represented on the same plant.

#### *External Features.*

The megastrobili occur terminally on the pectinate shoots;* as a rule solitary, they sometimes occur in pairs (Plate 11, fig. 22), and, according to BRONGNIART and GRIS (1869, p. 330), even in threes. Each strobilus is borne directly on a long peduncle, and consists of a large fleshy receptacle, ending in a single plum-like seed.† The photographs on Plate 11, figs. 22, 23, are natural size. At the stage represented, the peduncle is strongly curved, sometimes almost into a semicircle; it is completely covered with adpressed scale-leaves, each consisting of a basal cushion adnate to the axis, and a free triangular apex provided with a faint abaxial keel. The peduncle tapers slightly towards the base, for the cushions of the leaves diminish in size, while the keels become more prominent.

The receptacle, sharply marked off from the peduncle by a sudden increase in diameter, is 10–18 mm. long and 8–10 mm. in diameter, being slightly thicker distally. From its remarkably verrucose or tuberculate surface project the thick scale-like tips of a few distant sterile bracts. These bracts are probably in serial continuation with the scales on the peduncle, although their arrangement is obscured by the much greater length and swollen character of the internodes; at the base of the receptacle the sterile bracts are of a size and form transitional to the leaves on the distal part of the peduncle.

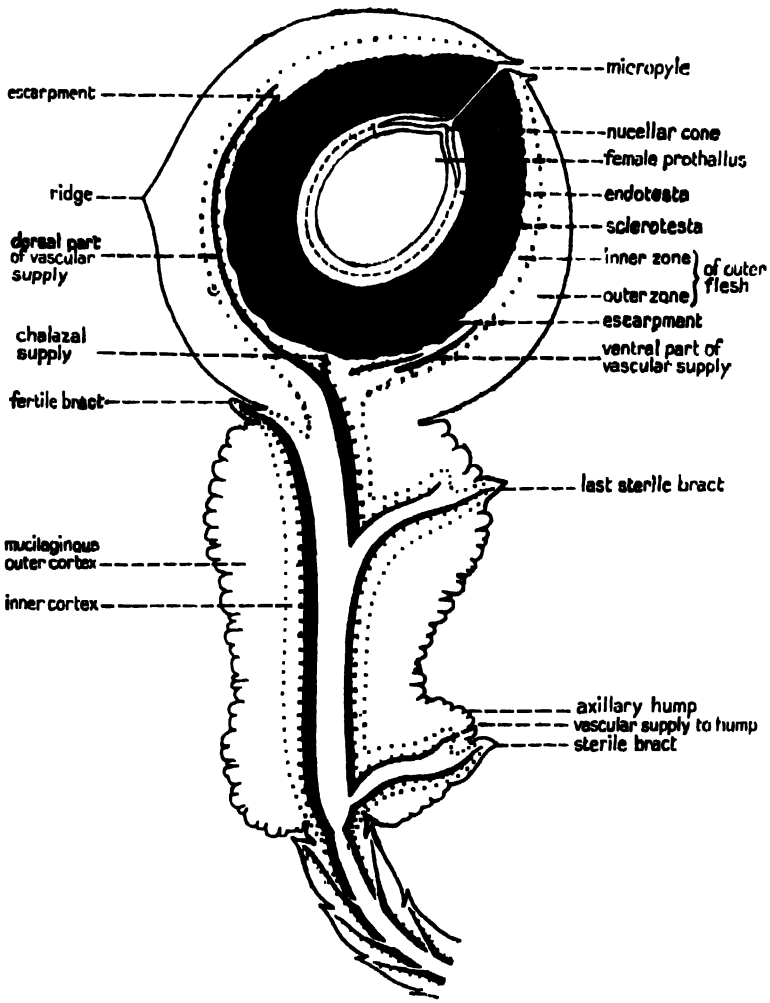
A feature worth noting is that in the axils of many of the sterile bracts the surface of the receptacle is raised into a more or less prominent hump (text-fig. 6), usually distinguishable from the swollen base of the bract. The entire receptacle is thus composed of the swollen axis, the swollen bract bases, and these axillary humps, which, to judge from their vascular supply, are probably vestigial axes (see p. 267).

Attention must be drawn to a curious fact constantly observed in the material at

* PILGER also records strobili in the axils of the distally situated smaller leaves.

† PILGER records 1–2 fertile bracts on each receptacle.

my disposal, namely, that the most distal sterile bract of each receptacle differs from the others in two respects. Firstly, the tip of the bract is awl-shaped instead of scale-like; secondly, the cushion bearing this free tip is considerably larger than the swollen bases of the other bracts, and is always circular with the bract-tip projecting from the centre (Plate 11, fig. 23, text-fig. 6). One face of the receptacle, conve-




TEXT-FIG. 6.—Diagrammatic longitudinal section, in the dorsi-ventral plane, of the peduncle, receptacle, and seed of *Acmopyle* (compare Plate 11, fig. 22*r*). The vascular bundles in the axils of the bracts are shown in the figure, although, being paired, they would not actually be visible in a median section. The *xylem* strands are shown as thick longitudinal lines, the *phloem* as short transverse lines.

niently called the dorsal, is usually free of sterile bracts (Plate 11, fig. 22*a*, is the only exception in my material); this is the side on which is situated, at the distal end of the receptacle, the single, smooth, broadly rotundate, fertile bract (Carpidium, PILGER), easily distinguished from the sterile bracts by its shape and, of course, by the fact that it subtends the seed. In Plate 11, fig. 22*a*, the fertile bract is seen wedged in between the receptacle and the seed. The most distal sterile bract is

always placed on the ventral side of the receptacle, directly, or almost directly opposite to the fertile bract.

Although in the absence of young material a definite opinion cannot be expressed, I rather incline to the view that the large round elevation on the ventral face of the receptacle is the organic apex of the strobilus, pushed aside and overtopped by the developing seed. The fertile bract would thus be not the most distal leaf on the receptacular axis. This conclusion is based chiefly on analogies in *Podocarpus* and *Dacrydium*. (See especially PILGER's figure of *D. Bidwillii* (1902, p. 47) and STRASBURGER's account of *Podocarpus chinensis* (1872, p. 20, and Plate 2, fig. 38)). Miss Gibbs also states (1912, p. 539) that in *P. spicatus* the apex of the strobilus is always distinguishable beyond the last fertile bract.

A similar pushing aside of a primary apex by an enlarging seed has been well known in *Taxus* since VAN TIEGHEM discovered it in 1869 (*loc. cit.*, p. 303, and Plate 16, fig. 91; see also STRASBURGER's well-known figure, 1872, Plate 1, fig. 5).

The unripe seed is an almost perfect sphere, sessile on the apex of the receptacle, with its axis inclined to that of the receptacle at an angle of about 45°. It thus presents a strong contrast to the condition in *Podocarpus*, but approaches that in some species of *Dacrydium*.

The seeds figured by PILGER (1902, p. 117) are all very nearly erect; this fact may quite possibly be due to his material being slightly older than that examined by me, and may suggest that the young ovule is horizontal or even further inclined, as in some species of *Dacrydium*. However, in the absence of younger material, these remarks can only be taken as conjectures. (See also p. 285, below.) It is worth mentioning that the seeds here described were collected in March, 1914, on Mount Mou.

The surface of the drupaceous seed is covered with bloom and is smooth except for a slight ridge passing obliquely round the base of the seed, but not forming a complete circle. If the seed is viewed from the ventral side (Plate 11, fig. 23), the ridge is hardly visible.

The micropyle is distinctly two-lipped, the upper lip adpressed, the lower projecting and transversely extended.

### *Anatomy.*

*The Peduncle.*—It was mentioned above that at the stage represented in Plate 11, fig. 22, the peduncle is strongly curved. The plane in which the curvature lies is by no means fixed with regard to the dorsal and ventral faces of the receptacle. In text-fig. 6 it *happens* to coincide with the dorsiventral plane. A section across the distal region of the peduncle shows a striking peculiarity: the strands composing one-half of the vascular ring are much stouter than the rest. This asymmetry was at first suspected to have a relation to the plane of curvature of the peduncle as a mechanical adaptation, either the convex or the concave side having the better developed strands. However, sections through peduncles curved in different planes soon showed that this is not the case: the best developed strands were invariably

found to lie along the line which if produced distally would pass along the dorsal face of the receptacle and through the fertile bract. It will later be seen that this want of symmetry in the vascular system is continued right through the receptacle itself, and that it is no doubt connected with the needs of the developing ovule.

*The Receptacle.*—(a) *Non-Vascular Tissues.*—The ground-tissue is rather sharply marked off into two concentric regions. The central area comprises the pith, medullary rays, and a few of the inner cortical cell-layers; it is characterised by the small size of the thin-walled longitudinally extended cells, by the entire absence of mucilage cells, and by the presence of small scattered "resin"-cells. The peripheral zone differs in the much larger size of the cells, which, moreover, are mostly radially elongated, and especially in the great preponderance of huge mucilage cells, which form the bulk of the outer cortex, and are responsible for the fleshiness of the receptacle. The large amount of mucilage in the receptacle and in the outer flesh of the seed very probably serves as food to birds, which no doubt disperse the seed. Hand-sections of the receptacle, when placed in water, swell up markedly in their peripheral region, while the central portion remains unaltered. The clear contents of the mucilage cells become white and opaque in strong alcohol; they are slow in taking up stains, and show a granular or alveolar structure. "Resin"-cells are also present in the outer cortex; they are larger and more abundant than in the pith, and, like the mucilage cells, are radially elongated, frequently forming radial chains (Plate 10, fig. 13).

Fig. 13, Plate 10, shows the rather deeply lobed appearance of the tuberculate surface of the receptacle. A specially thick cuticle covers the spherical ends of the lobes, and the small-celled epidermal layer is exceedingly rich in the dark-brown "resinous" matter. No stomata were observed on any part of the receptacle.

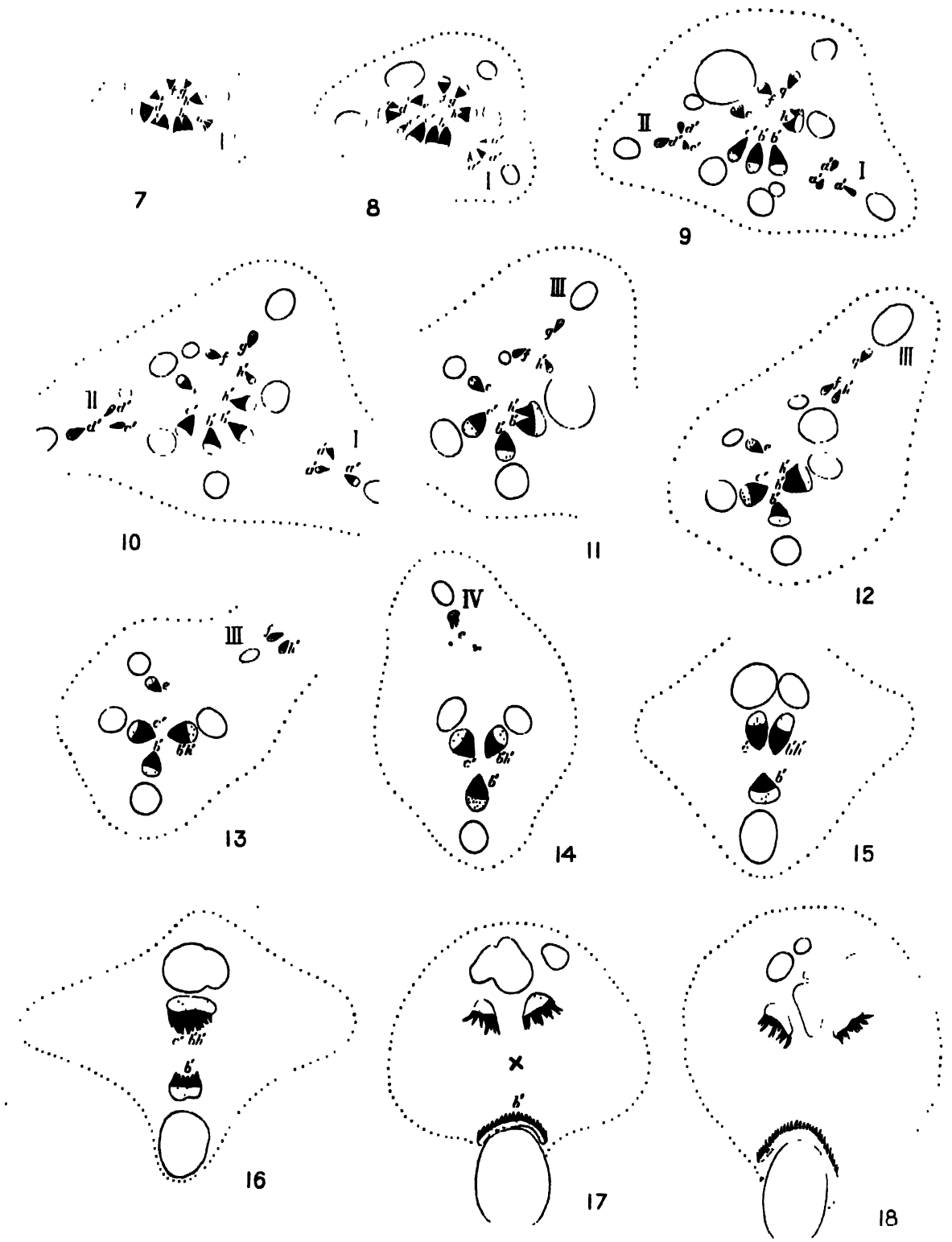
The free tips of the sterile bracts have a thick cuticle perforated by a few stomata on both faces of the bract. In the fertile bract the lower cuticle is considerably thicker than the upper, both being pierced by irregularly distributed stomata.

(b) *Vascular Anatomy of the Receptacle.*—Of all the known Podocarpineæ the vascular system of the receptacle is the most complex in *Acmopyle*. In broad outline it may be described as a dictyostele from which a simple leaf-trace is given off to supply each of the bracts, and in typical cases two strands come off from the sides of the leaf-gap to supply the humps in the axils of the bracts.

The following account is based chiefly on complete series of transverse sections of three whole receptacles and portions of two others. Of these one was embedded in paraffin after most of the cortex had been removed, and was microtomed from base to apex.

A description will first be given of one of the receptacles, then the more important variations observed in the others will be dealt with.

Serial sections cut from the distal end of the peduncle and carried up into the base of the receptacle show at the junction between the two regions a slight constriction in




TEXT-FIGS. 7–18.—Vascular anatomy of the receptacle of *Acanopale*, as revealed in serial transverse sections from the base upwards. *Xylem*, black; *phloem*, dotted. The peripheral dotted line represents approximately the limit between the inner and outer cortex. In all the figures the dorsal (posterior) side of the receptacle faces the foot of the page. Further explanation in the text.

the pith, which suddenly expands again distally, though not in proportion to the enormous increase in diameter of the receptacle as compared with the peduncle Text-fig. 7, from the base of the receptacle, shows a ring of about eight collateral endarch strands of which those lying on the posterior side are distinctly the largest. Surrounding the strands is a ring of seven mucilage canals, one outside each strand, except for one of the strands which is without a canal.

The receptacle in question had four sterile bracts; three of these had each a well-developed axillary hump; the fourth and most distal arose, as already described, from the summit of a relatively large circular prominence on the ventral face of the receptacle. In the figures the Roman numerals refer to the vascular supplies of these sterile bracts in acropetal order. It is not always easy to speak, in definite terms, of the exact number of strands in the axial cylinder for, as the diagrams show, several of them are in different stages of fusion and disintegration; but it is hoped that the letters adjoining them will enable the reader to identify the strands, or their components at different levels, without unnecessary reference to the text.

Sterile Bract I: Strand *a* comes off bodily from the ring, causing in the latter a gap which closes up in text-fig. 11. The strand immediatelly splits up radially into three pieces which soon arrange themselves fanwise, the canal of the original strand being at the back of the middle piece. This arrangement is brought about by the two lateral pieces turning away from the median with their protoxylem ends as pivots. As we trace the little system obliquely upwards through the cortex of the receptacle the two lateral strands continue their turning movement till they have almost completely reversed their orientation (fig. 10). While the normal median strand with its canal enters the free tip of the sterile bract, there ending in a mass of transfusion tracheides, the two inverted strands end blindly in the mass of small-celled tissue forming the core of the axillary hump. Between the paired inverted strands supplying the axillary hump and those supplying a normal vegetative axillary branch (text-fig. 5) there is such a close resemblance that the hump appears without doubt to be a reduced axillary shoot. See also p. 293 below.

Sterile Bract II: The supply to this bract comes off at only a slightly higher level than that to the first. As before, one of the strands in the ring (*d*) passes out bodily, but in this case it splits up into two unequal pieces (*d'*, *d''*) of which the larger enters the bract-tip. The supply to the axillary hump is in this case formed partly by the smaller piece, and partly by a branch (*c*) from one of the strands of the axial ring. The behaviour of the pair of axillary strands is precisely the same as that already described under Sterile Bract I.

Sterile Bract III: At this stage we have reached a level in the receptacle midway between its base and apex; meanwhile the remaining strands of the ring have undergone considerable re-arrangement which will be clear from the lettering in the figures.

The strand *g* passes out from the ring (fig. 9) and without dividing enters the

bract-tip. The supply to the axillary hump consists as before of two strands (*f*, *h'*). Of these one (*h'*) arises, as in the case of the second bract, by the splitting of one of the strands at the sides of the leaf-gap; the other is constituted by the entire strand (*f*), flanking the other side of the leaf-gap. These two axillary strands behave exactly like those in the axils of Bracts I and II, except that, being appreciably larger than the former, each of them at the same time carries out with it a mucilage canal (fig. 12). These two canals very soon fuse into one (fig. 13).

Sterile Bract IV: We are now near the apex of the receptacle; there is a ring of four strands, three of them much the largest. The smallest of these (*e*), occupying the ventral side of the ring, forms the supply to the fourth sterile bract and its associated hump, which, it will be remembered, is larger than the other humps. The strand passes out undivided through about half the thickness of the cortex, and then gives off from its upper surface two minute strands whose orientation it was not possible to determine (fig. 14). The subsequent behaviour of these strands leaves little doubt as to their homology with the inverted axillary strands above described (see text-fig. 10).

Fertile Bract: There are now three very large strands in the axis (fig. 15). If we trace these strands or their components downwards to the base of the receptacle, we find that the posterior one (*b'*), which is the trace of the fertile bract, has all along preserved its original orientation (text-figs. 7–9). On the other hand, the components of the other two strands (which in fig. 13 face each other, lying in the right-left plane) originally formed part of a more open ring.

As we proceed distally (towards the base of the seed), the two opposing strands continue their turning movement till they come to lie parallel to each other, diametrically opposite both in position and orientation to the third strand. These "inversely orientated" strands compose the vascular supply of the seed; their further behaviour will more appropriately be described later, but attention may be directed to their obvious homology with the paired strands in the axils of the sterile bract-traces. Their relatively huge size is evidently connected with the nutrition of the seed, which may be said to exercise a basipetal influence, which is felt as far back as the peduncle, and results in the asymmetrical development of the entire vascular cylinder.

Shortly before entering the fertile bract, the trace becomes much extended tangentially, and tends to spread round the large mucilage canal, narrow "medullary" rays at the same time breaking it up into a number of thin plates. In the distal part of its course, transfusion tracheides appear in large quantities.

*Variations Observed in other Receptacles.*—(1) In each of the other two receptacles, which were sectioned from base to apex, the trace of the first sterile bract was not accompanied by any axillary strands.

(2) The last sterile bract of one of these receptacles possessed two unusually large axillary strands, each of which became inversely orientated during its outward

passage, and carried out with it the associated mucilage canal. The two canals did not fuse into one, as described above under Sterile Bract III, but ended blindly shortly before the strands themselves.

(3) The last sterile bract of the other receptacle had only one axillary strand, of medium size, and accompanied by a canal. The behaviour of this single axillary strand was exactly the same as if it were one of a pair, for it did not occupy a median position, and, during its outward course, rotated through an angle of nearly 180°.

In order to check the results obtained from transverse sections, portions of the fourth and fifth receptacles were embedded in paraffin for longitudinal sections, as well as for sections cut transversely to the oblique course of the bract and axillary strands. An axillary strand, as seen in longitudinal section, is shown in text-fig. 6. Turning slightly upwards, in the distal part of its course, it ends blindly in the midst of the small-celled core of the hump.

*The Seed.* (a) *Non-vascular Structures.*—Text-fig. 6 shows a median section of the unripe seed along the dorsi-ventral plane, which is the only plane of symmetry. The oblique curved ridge on the back of the seed is crossed by this plane about two-fifths of the way up from the fertile bract to the micropyle. The surface of attachment to the receptacle is considerably broader than appears from PILGER's fig. 24*b* (1903, p. 117). PILGER, moreover, figures the seed as being very nearly erect (see his fig. 24*c*); the stony layer is shown proportionately much thicker than it is in any of the seeds examined by me, while the outer flesh is represented as little more than a skin covering the stone, probably because PILGER examined dried material.

The fleshy outer coat of the seed has a roughly uniform thickness of about 2–2·5 mm., except near the apex of the seed. Here it rather abruptly thins to about 0·5 mm., and forms the distal one-third of the micropylar canal. This part of the canal is peculiar in its curved horn-like shape (text-fig. 6), the curvature being in the plane of the section figured. Moreover, this part of the canal traverses the seed-coat very obliquely, being bent at a considerable angle (over 60°), to the straight inner part of the canal, which is bounded by the sclerotesta.

A very thick cuticle forms a smooth protective covering pierced by stomata, which are consequently more deeply sunk than those on the leaf. The distribution of the stomata, which are, as a rule, placed longitudinally, does not show any regularity, except that they are, on the whole, perhaps fewer towards the micropylar end. The lumina of the epidermal cells are small, and nearly always filled with the brown substance above mentioned. At the micropyle the epidermis dips inwards, to line the horn-like part of the canal, the cuticle at the same time gradually becoming thinner.

The fleshy outer coat of the seed is roughly divided into a thick outer zone exceedingly rich in mucilage cells and devoid of vascular tissue, and a thinner

layer immediately covering the sclerotesta. This zone appears much darker than the outer, because it almost entirely consists of "resin"-cells. *The vascular system of the seed is confined to the inner zone.*

The stony layer has a thickness about equal to that of the outer flesh at the seed-base, and encloses a cavity whose diameter almost equals the combined thickness of the stony and outer fleshy layers.

The inner surface of the stone is smooth, but the outer is carved into a pattern which although complex is essentially constant. The photographs on Plate 10 (figs. 15–19) will give a better idea of the sculpturing than will be obtained from a lengthy description. They represent different views of one seed from which most of the flesh was scraped off. The darker lines and patches correspond to the depressions in the surface, from which the remains of the "resinous" inner zone of the flesh could not easily be removed. The surface of the stone is sharply marked off into two regions, an apical and a basal, by a line which may be described as an escarpment facing the micropylar end. (See the sectional view in text-fig. 6.) It will be noticed that while the apical region is characterised by a uniformly granular surface, the basal region shows a series of thick dark lines diverging from the chalaza and ending abruptly at the escarpment. These irregular lines are due to grooves in the stone, and represent the course of the more important vascular strands in the inner region of the outer flesh.

The "escarpment," as seen in the sectional view (text-fig. 6), rather suggests the so-called "crown" which forms the most obvious distinctive feature of the palæozoic seed, *Stephanospermum*. The resemblance is not so clear with *S. akenioides*, Brongn., as with *S. caryoides*, Oliver, where the crown being much less developed, the peri-micropylar trough is shallower (Oliver, 1904, p. 380, text-fig. 2). The comparison is, however, only permissible so far as the longitudinal section is concerned, for while in *Stephanospermum* the edge of the crown forms a complete circle which lies in a single plane transverse to the seed-axis, in *Acmopyle* the line of the escarpment forms two wide loops, one on the ventral face of the stone, the other on the dorsal. These loops, of which the ventral is considerably the deeper, are only narrowly connected together at the micropyle.

It will be seen from text-fig. 6 that the position of the escarpment has no relation either to the ridge on the external surface of the seed, or to the line of separation of the nucellus from the integument.

Prof. Oliver (1903, Plate 24, fig. 13) also figures in *Torreya* a rather similar line on the surface of the stone, but this, as he states (p. 468), marks the line of separation of the integument from the arillus.

According to Sprecher (1907, p. 123, fig. 123), in *Ginkgo biloba* the line of separation of the nucellus and integument is marked by a circular groove on the outer surface of the stone at a level below that of the equator. I am, however, unable to confirm this observation in some material of this plant from Montpellier.

In its symmetry, so far as I know, the stone of *Acmopyle* is unlike that of any other Gymnospermous seed hitherto described. The two faint ridges on the right and left sides (Plate 10, figs. 18, 19), correspond to those on a bicarinate seed of *Ginkgo* or *Taxus*, in which genera they lie in the plane of principal symmetry; but in *Acmopyle* the plane in which the ridges lie is not flat but distinctly curved with the convexity facing the dorsal side (see the side view, Plate 10, fig. 18). An examination of the photographs will show that the chalaza of the stone—if one may employ this term for the point from which the strands radiate—is not situated exactly at the broad end of the stone, so that the straight line joining the micropyle with the chalaza does not represent the greatest length of the stone. The eccentric position of the chalaza is well demonstrated by Plate 10, figs. 15 and 17, which are respectively ventral and basal views. In a view from the dorsal side (fig. 16) the chalaza is not visible. Thus it happens that what in numerous other Gymnospermous seeds corresponds to the plane of principal symmetry, is in *Acmopyle* not a plane of symmetry at all. As is the case with the entire seed, the median dorsi-ventral plane is the only plane of symmetry.

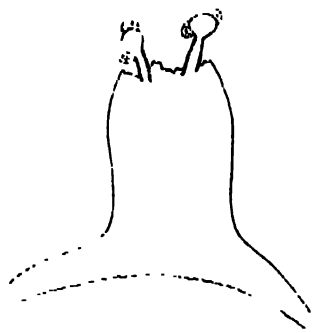
Viewed from either the front or the back the stone has an almost circular outline, there being hardly any trace of a micropylar beak. A section across the middle is isodiametric (Plate 11, figs. 20, 21); the cavity of the stone is here nearly circular, but it is noteworthy that the plane of dehiscence does not traverse it symmetrically, the ventral valve being distinctly larger than the dorsal (text-fig. 32). This asymmetry tends to disappear towards the distal part of the stone. A section across the apical region is lemon-shaped (text-figs. 33, 34), the stone being here slightly flattened in the right-left plane, and produced at each side into a blunt ridge. The portion of the micropylar tube bordered by the sclerotesta is about 2·5 mm. long; throughout this region it is a narrow slit-like passage, flattened in the dorsi-ventral plane (text-fig. 34), and immediately lined by one layer of "resin"-cells continuous with the epidermal lining of the more distal portion of the canal. Meeting this slit at right angles, and joining together the two ridges on the stone are two faint lines representing the plane along which the stone probably dehisces during the germination of the seed.

The cells composing the stone are generally isodiametric, except those along the plane of dehiscence which are flattened in that plane, and those along the cavity of the stone which are flattened tangentially. Their walls are pierced by numerous fine branched canal-like pits which as usual correspond in position on the opposite sides of the middle lamella. In SCHULTZE's solution the main substance of the wall becomes yellow, but the innermost lining of the cell—which in surface view presents a sieve-like appearance—as well as the lining of the pits, gives the cellulose reaction.

As in *Podocarpus* the inner fleshy layer is for the most part fused to the nucellus (text-fig. 6). The limit between the two is difficult to make out in the fused region, except for the presence, in the inner flesh, of scattered "resin"-cells which increase

in number towards the sclerotesta, and even encroach upon the adjacent regions of the latter. The innermost layer of the free portion of the inner flesh consists largely of "resin"-cells, and is continuous with the rather similar lining of the micropylar canal which may hence be regarded as representing the inner flesh in that region.

The free portion of the nucellus is dome-shaped, and its apex is produced as in *Podocarpus* into a distinct receptive cone or column traversed by several rather thick-walled empty pollen-tubes (text-fig. 36). The nucellar cone, as well as the upper part of the dome upon which the cone is perched, appears white in contrast to the lower part of the dome, whose superficial layer of cells is rich in "resin" (Plate 11, fig. 25). A definite layer of cuticle protects the entire free region of the nucellus except the very tip of the nucellar cone where the cells are crushed and disorganised (text-fig. 36).



TEXT-FIG. 36. The receptive column of the nucellus of *Acmopyle*, with germinating pollen-grains. The shaded apical portion of the nucellus has become disorganised.

The apex of the female prothallus forms a blunt conical process which lies against the base of the nucellar cone (text-fig. 6 and Plate 3, fig. 26), suggesting the so-called "tent-pole" of *Ginkgo*, *Cordaites*, and other archaic Gymnosperms (BRONGNIART, 1881, Plate 2, fig. 2; Plate 3, fig. 8; Plate 6, fig. 9; Plate 11, fig. 4; Plate 12, fig. 2). The pro-embryo has already been formed; no traces are seen of any aborted archegonia. From the position of the single pro-embryo it may be inferred that the parent archegonium opened a little to one side of the central axis (Plate 11, fig. 26). It may be stated that one prothallus showed an embryo exactly in the axis. In the distended condition of the archegonial wall jacket cells, if there were any in the young archegonium, are not visible.

The structure of the pro-embryo and suspensor tubes presents no features of special interest, being practically identical with that in *Podocarpus*. I am unable to say whether there is a sterile cap to the embryo, such as SINNOTT describes in some species of *Podocarpus* (1913, p. 60).

PILGER (1903, p. 33) records unusually long suspensor tubes in some species of *Podocarpus* (*P. amarus*, 30 mm.). In *Acmopyle* the tubes when stretched out reach a length of over 15 mm.

As in most species of *Podocarpus*, too, the megaspore membrane is poorly developed (Plate 11, fig. 28), although it is possible to distinguish two layers, of which the outer is a film of cuticle. On the conical apex of the megaspore the membrane is particularly thin, the cuticle being absent, or at any rate extremely thin.

Plate 11, fig. 28, shows a longitudinal section of the superficial region of the female

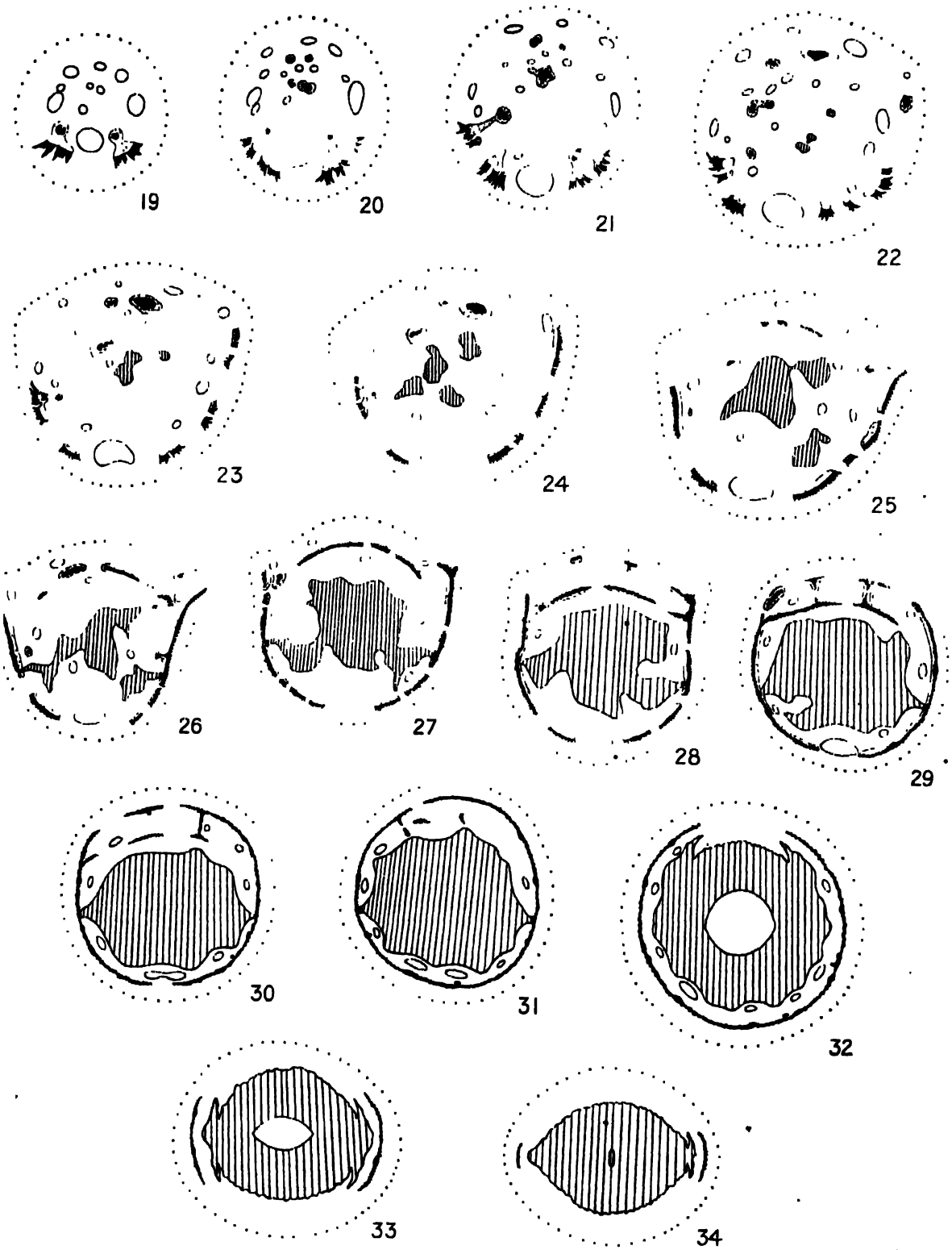
prothallus; the small multi-nucleate cells (see Plate 11, fig. 29) composing the peripheral layer of the prothallus have their anticlinal walls slightly thickened in the regions adjacent to the megaspore membrane. In the last-mentioned figure, which is a surface view of this layer, these walls are seen traversed by straight pits.

All the remaining cells of the prothallus are thin-walled and most of them are multi-nucleate: those forming the axis of the prothallus in front of the advancing embryo are distinguished by their small size, elongated shape and abundant starch-content. No tracheides were seen such as those described by Miss GIBBS (1912, p. 546, Plate 51, figs. 42–3) in *Podocarpus polystachya* and by COKER (1902, p. 97) in *P. coriacea*.

(b) *Vascular Anatomy of the Seed.*—In broad outline the vascular structure of the seed may be described as a tracheal cupule (Plate 11, fig. 24) stiffened by a network of strands and exactly covering the basal region of the stone which, as already mentioned, is limited distally by the "escarpment." A vascular system internal to the stone is not present, but besides two concentric strands terminating against the chalazal end of the stone, a number of other strands come off at different levels from the inner surface of the cupule, and end before reaching the sclerotesta. In the right-left plane the tracheides of the cupule are for some distance in organic connection with the stone cells.

The vascular system will now be described in detail (text-figs. 19–34). Text-fig. 35 shows the approximate levels at which the sections drawn in text-figs. 19–34 were cut. Serial transverse sections were cut of two seeds, and the results confirmed by dissections and longitudinal sections of two others. A reference to fig. 15, p. 266, will show that at the apex of the receptacle there were two very large strands lying parallel to each other and with an orientation inverse to that of the fertile bract-trace. We shall now examine the further behaviour of these strands, for it is chiefly by the disintegration of these that is produced one of the most complex vascular systems known among Gymnospermous seeds.

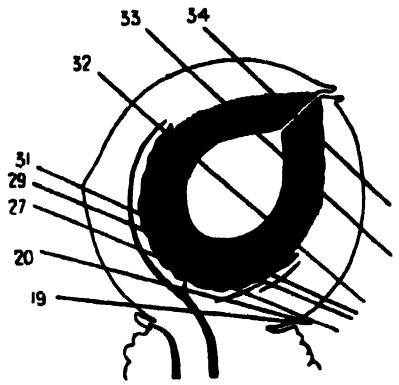
Immediately above the level where we left them on p. 268 these two strands completely fuse together, xylem with xylem and phloem with phloem, while their mucilage canals may also fuse into one (text-fig. 16). However, the resulting large strand immediately breaks up again into two (text-fig. 17); at the same time the two mucilage canals (or one in case of fusion) are replaced by several canals of different sizes which lie in two roughly concentric rings (text-fig. 19). At this level an important change has taken place in the aspect of the cross-section; whereas at first the centre of the figure was towards the xylem side of the strands (at × in fig. 17) it has now shifted suddenly to the phloem side, and lies in the middle of the group of mucilage canals (fig. 19). The cells among which the canals lie are distinguished from the surrounding tissue by their small size, and by the fact that they are nearly all filled with "resin." We are now at the chalazal end of the seed, and these cells constitute the dark internal zone of the fleshy seed-coat, of which the outer limit is




TEXT-FIGS. 19–34. Vascular anatomy of the seed of *Acmopyle*, as revealed in serial transverse sections. *Xylem*, black; *phloem*, dotted. The peripheral dotted line represents the limit between the two zones of the outer flesh. In all the figures the dorsal (posterior) side of the seed faces the foot of the page. *For the approximate levels at which the different sections were cut, see the corresponding numbers in text-fig.* 35.

marked in the figures by means of a dotted line. Nevertheless, it must be made clear that the boundary is by no means a sharp one.

As we trace the two strands upwards, they diverge from each other, especially by their xylem ends, and at the same time become tangentially extended. One or more radial splits soon appear in the xylem, so that for a time each of them consists of an unbroken mass of phloem facing the centre, and a forked mass of xylem directed outwards.




TEXT-FIG. 35.—Index-figure to text-figs. 19–34.

At about this stage two fairly large concentric strands come off, one from the inner face of each, but they soon dwindle in size, and, before they have proceeded very far towards the centre, they end blindly near the chalazal end of the stone. They are probably the reduced homologues of the two strands in *Ginkgo* which, lying in the principal plane of the seed, penetrate the base of the sclerotesta.

The splits in the xylem of the two large original strands rapidly extend to the phloem, and result in the formation of several distinct strands, which in turn become tangentially flattened, and split up radially into a large number. These tend to envelop the central tissue, including the mucilage canals, amongst which by now the first traces of the stony layer have also appeared (text-figs. 22, 23). This process of fragmentation, accompanied by tangential flattening of the strands, ultimately gives rise to the thin but nearly continuous vascular arc, which, at the level shown in text-fig. 27, covers the dorsal two-thirds of the cross-section.

The similar arc forming the ventral one-third of the vascular ring in the same figure has originated independently of the dorsal arc. In order to trace its mode of origin, we must again refer to the series of sections in text-figs. 19–27. In text-fig. 20 it will be noticed that there is, besides the large dorsal strands, a group of small mostly concentric strands on the ventral side of the section. In the small amount of material examined I could not trace any connection at the chalazal end between the dorsal and the ventral groups. As this fact was subsequently found to be of some theoretical importance (see p. 283, below) in the interpretation of the seed of *Acmopyle*, it was considered worth while to confirm it by means of paraffin sections of the basal region of a third seed (in addition to the two sectioned by hand); no trace of a connection was observed. The ventral strands are in two batches, one inside the inner ring of canals, the other in the space between the two rings. Those of the inner batch terminate after only a short upward course; those of the outer batch, on the contrary, increase in number, and, becoming markedly flattened in the tangential direction, ultimately form the ventral arc seen in text-fig. 27.

Thus, at the level of the figure just referred to, the stone is almost completely

enveloped by two vascular arcs. The ends of the dorsal arc become distinctly curved outwards (text-figs. 26–28), and it is noteworthy that these reflexed ends correspond in position to the ridge on the outer surface of the seed. The dark internal zone of the fleshy seed-coat also shows distinct bulges over these curved ends. So far as I could ascertain, no other disturbance is caused by the ridge in the internal structure of the seed.

As we proceed distally, new strands make their appearance outside the ventral arc, and these establish connections both internally with the ventral arc and laterally with the free ends of the dorsal arc (text-figs. 28 30). For a short distance upwards there are thus two interrupted ventral arcs, which are connected together by radial commissures, and which at their ends converge into the single dorsal arc (text-figs. 29–30). The inner ventral arc now rapidly breaks up and dies out, while the outer at the same time becomes more substantial, with the result that the stone is soon enveloped by a single, practically unbroken, vascular ring (text-fig. 31). In this ring the local thickenings are the transverse sections of the compressed, ill-defined strands, which may be said to form a supporting network for the vascular cupule shown in surface view in Plate 11, fig. 24.

The figure just referred to is from a slightly enlarged photograph of the left half of a seed, from which the outer portion of the fleshy seed-coat was carefully shaved off, so as to expose the tracheal cupule. The photograph was taken with the seed immersed in alcohol, for the cupule then assumed a white colour, and stood out clearly against the dark inner zone of the flesh. At the base are the two large strands forming the main supply. A comparison with the side view (Plate 10, fig. 18) of the naked stone shows that the edge of the cupule closely follows the line of the escarpment. This correspondence is well seen in the sections shown in text-figs. 32–34. As we proceed towards the distal end of the seed, two successive gaps appear in the cupule: first, a gap corresponding to the ventral (deeper) loop of the escarpment (text-fig. 32), and, at a higher level, another corresponding to the dorsal loop (text-fig. 33). The gaps rapidly enlarge, so as to reduce the cupule to two lobes, opposite to the right and left ridges of the stone. These lobes extend up to within a short distance of the micropyle, becoming narrower and narrower as they approach the apex of the seed (text-fig. 34).

At various levels the inner surface of the vascular envelope gives off minute strands towards the sclerotesta, but all of these die out before actually reaching it. Plate 11, fig. 21, is a photograph of a section cut at about the level of text-fig. 32.

Text-figs. 26–33 show a feature worthy of special note, whose importance will be seen in the theoretical part of the paper (p. 286): along two lines which lie in the right-left plane of the seed, the cells composing the stone are for some distance in intimate contact with the tracheides of the cupule. This liaison between the vascular system and the sclerotesta, coupled with the porous structure of the latter, suggests that the sclerotesta may to some extent serve to keep up a supply of water to the

developing female prothallus and embryo. This view seems all the more probable in the absence of a vascular system internal to the sclerotesta. In *Ginkgo*, where there is no vascular system outside the sclerotesta, SPRECHER (1907, p. 137, fig. 150) has drawn attention to the remarkably tracheide-like character of the superficial cells of that layer.

Fig. 27, Plate 11, gives some idea of the different shapes and sizes of the tracheides composing the cupule. While the majority of the tracheides are long, narrow, and generally placed lengthwise, some are broader and nearly isodiametric. The sculpturing is difficult to describe, being of various types grading into each other, but the general impression gained is that of the transfusion tissue of the leaf. Special mention may be made of the occurrence of spiral tracheides, some of which have several bands crossing each other; minute round pits may also be present on these, as they may be on all the remaining types of tracheides composing the vascular investment.

Before closing the description of the seed, it must be stated that in the vascular cupule the position of the phloem with regard to the tracheides could not always be determined with certainty, and that for this reason it was considered best to omit the phloem altogether from some of the drawings (text-figs. 30–34). In text-figs. 28, 29, too, the amphi-phloic nature of the ventral strands is by no means certain. The exceedingly hard sclerotesta makes thin sections impossible, while the preponderance of "resin"-cells tends to obscure the vascular tissues embedded among them.



TEXT-FIG. 37.—Part of transverse section of vascular cupule from the seed of *Acmopyle*. The outer face of the cupule corresponds to the lower edge of the figure. The thick-walled cells are tracheides, the thin-walled cells phloem, the latter being mostly internal to the xylem. In the middle of the figure some tracheides are coming off from the inner face of the cupule. Sculpturing of tracheides not shown.

It appears likely, however, that the major portion at least of the cupule has only an internal lining of phloem—a condition which would be in harmony with the inverted orientation of the ovular supply in *Podocarpus* (see text-fig. 37).

Finally, it may be noted that the mucilage canals—one of which elsewhere in the plant generally accompanies each strand—in the seed have a distribution which is at present not reducible to a definite principle, except that in the distal half of the seed, at least, they all lie in a ring between the sclerotesta and the cupule. Their position

inside the cupule is in conformity with their usual association with the phloem side of strands.

*Theoretical.*

From the foregoing description of *Acmopyle* it will be agreed that the plant shows some obvious resemblances to *Podocarpus*, the genus to which the discoverer, PANCHER, originally assigned it. The points of resemblance are indeed so numerous and far-reaching that to some systematists it may even appear doubtful whether a generic separation is justified.

Thus the habit, as well as the stem and root structure, including the wood-anatomy and the presence of root-nodules characteristic of the family, are features common to the two genera. The intimate correspondence shown by the two genera in the habit and structure of the male cones and microsporophylls, as well as in the outward form of the pollen-grain, fully justifies the presumption that the same will be found to be the case with the male gametophyte, an important structure which shows, so far as known, a remarkable constancy of plan throughout the Podocarpineæ. In the female organs, too, the thick fleshy receptacle, and especially the drupaceous seed, with the semi-inferior nucellus and the structure of the pro-embryo, find their exact counterparts in *Podocarpus*.

Although the receptacle of *Acmopyle* shows the most complex organisation known among the Podocarps, it does not present a single feature of importance not also met with in *Podocarpus*; and in this respect, so far as I have been able to ascertain, the nearest approach to *Acmopyle* is seen in the § *Dacrycarpus*. On a minute scale, the receptacle of *P. imbricatus*, Bl. (= *P. cupressinus*, R. Br.) recalls that of *Acmopyle*, both in the verrucose or tuberculate surface (Plate 11, fig. 30) and in the vascular anatomy.*

There is at the base a vascular cylinder composed of strands which as in *Acmopyle* are best developed on the side from which at a higher level the ovular supply originates. Paired axillary strands are also associated with some of the spirally disposed bract-traces; the members of each pair after their departure from the axial cylinder execute the familiar rotatory movement, but before completely reversing their orientation end blindly in the axil of the subtending bract. Strands which are no doubt homologous with these have been observed also in *P. spinulosus* (BROOKS and STILES, 1910, Plate 21, fig. 12); in *P. sinensis* (VAN TIEGHEM, 1869, Plate 15, fig. 82); and an unnamed species of *Eupodocarpus* (AASE, 1915, p. 303, fig. 173).

Here we may also mention that the superficial sculpturing of the stone of *Acmopyle* is very similar in pattern to that in a hitherto unpublished New Caledonian species of *Podocarpus* discovered by Prof. R. H. COMPTON. The photograph on Plate 11, fig. 31, will show that, as in *Acmopyle*, the surface of the stone is divided by an escarpment into two areas, although in this case the loops of the escarpment are

* To judge from herbarium specimens and published figures of the external features, *P. dacrydioides* would probably be essentially similar.

deeper than in *Acmopyle*. In a deep-lying structure a resemblance of this kind, apparently of no biological significance to the plant, cannot easily be explained away on the view of parallel development.

Next to *Podocarpus*, *Dacrydium* is the genus which most nearly approaches *Acmopyle*, for several of the above-mentioned *Podocarpus*-like features of *Acmopyle* are also met with in *Dacrydium*. The most obvious point in which the two last-named genera agree is, of course, the sub-erect position of the seed, which is at the same time a notable difference from *Podocarpus*, and it is significant that BRONGNIART and GRIS regarded *Acmopyle* as a species of *Dacrydium*.

Only three characters stand out prominently in *Acmopyle* as being distinct from *Podocarpus*. But they are all of sufficient importance to deserve careful attention, for upon their interpretation largely depends the position of *Acmopyle* within the family :—

*Firstly*, the vascular structure of the seed is peculiar.

*Secondly*, the ultimate posture of the ovule is different from that in *Podocarpus*.

*Thirdly*, the rather perplexing fact that there is, to all appearance at least, no sign of an epimatium.

These points will now be discussed in some detail.

### A. *The Interpretation of the Structure of* Acmopyle *in Relation to its Affinities.*

#### 1. *The Epimatium.*

The reader will have noticed that in the descriptive section of this paper no mention was made of an epimatium. This was not because an epimatium is lacking in *Acmopyle*, but because it does not figure as a distinct structure and, consequently, its existence is only inferred from a comparison with related genera. The obvious resemblance to *Podocarpus* and *Dacrydium* naturally lead one to seek a place for *Acmopyle* in the vicinity of those genera, and there is no escape from the conclusion that an epimatium must be present in this genus ; the real problem is to define its limits.

Before we attempt this in the case of *Acmopyle* it is necessary to be clear as to the limits of the epimatium in *Podocarpus* itself. It is well known that in a median longitudinal section (see Plate 11, fig. 30) the ovule of *Podocarpus* shows on the dorsal* side, near the micropyle, a distinct lobe (the free portion of the epimatium), of which there is no counterpart on the ventral (fused) side. The question arises as to whether :

(*a*) The " ovular stalk," adnate to the ventral side of the ovule, should be regarded

* To avoid confusion, it may here be stated that if the ovule of *Podocarpus* is conceived of as being adnate by its entire length to a stalk, the ventral face of the ovule is naturally understood to be that by which the ovule is fused to the stalk. This terminology is consistent with that applied above in describing *Acmopyle*, and may be extended to the other Conifers with inclined or inverted ovules, and even to the anatropous ovules of Angiosperms.

as a part of the epimatium, and the latter therefore as completely surrounding the ovule (PILGER, 1903, p. 16 ; TISON, 1909, p. 147 ; SINNOTT, 1913, p. 41 ; GIBBS, 1912, p. 527 ; STILES, 1912, p. 472) ; or

(*b*) The "ovular stalk" should be regarded as a structure distinct from the epimatium, in which case the latter does not completely surround the ovule.

On the first view the epimatium is homologous with the ovuliferous scale of other conifers ; on the second view only the "ovular stalk" with its distal continuation the "apical knob" (SINNOTT) is homologous with the ovuliferous scale. It is not easy to choose between the two views. In the absence of a histological differentiation between the stalk and the epimatium (in the restricted sense), it would be simpler to regard the entire structure in question as an ovuliferous scale whose margins have become arched over the seed so as completely to enclose the latter. But for convenience of description it is here considered preferable to employ the term epimatium in the restricted sense.*

While it may be immaterial whether the epimatium is regarded as completely surrounding the ovule, it is of real importance to have some idea as to the boundary between the integument and the epimatium which overlies it. The importance of this enquiry becomes apparent when we realise that STILES regards the vascular system of the seed of *Podocarpus* as being entirely epimatial rather than (in part at least) integumental, and that he denies its homology with the vascular system of the other Gymnosperms (STILES, 1912, p. 477).

Since this question is intimately connected with the morphological status of the vascular supply, the full discussion will be given at a later page. Here I will merely state that I consider it more natural to regard the inner part of the outer flesh, which contains all the descending strands, as an integral part of the integument. The epimatium of *Podocarpus* is on this view only the peripheral portion of the flesh and contains no vascular supply.

We are now in a position to attempt an interpretation of the seed of *Acmopyle* in terms of that of *Podocarpus*, its nearest ally. Two views present themselves ; one of them tends to relate *Acmopyle* more to *Dacrydium*, the other to *Podocarpus* :—

(*a*) The epimatium exists in the form of a broad concave scale, similar in shape and position to the epimatium in most species of *Dacrydium* (that is, forming a small asymmetrical cup at the base of the seed), but different in being fused to the integument by its entire inner surface. Its presence is outwardly indicated only by its margin, which forms the ridge (see Plate 11, fig. 22*a*) obliquely girdling the seed-base.

* This restricted use of the term epimatium would, indeed, be a necessity, if it is shown that the close analogy between the ovule of *Podocarpus* and the anatropous ovule of the Angiosperms is based on a homology of the different parts. For, the outer integument of the angiospermous ovule (which would then be homologous with the epimatium), is naturally regarded as a structure distinct from the funiculus, being frequently distinguishable also on the ventral side of the ovule, between the funiculus and the inner integument.

The semi-erect posture of the seed, which may be regarded as an important point of contact with *Dacrydium*, lends countenance to this view, and in virtue of its several *Podocarpus*-like features, *Acmopyle* deserves an independent generic position, bridging the gap between *Dacrydium* and *Podocarpus*. It is significant in connection with this view, that BRONGNIART and GRIS (1869, p. 330), regarded the plant as the only species of *Dacrydium* provided with a drupaceous seed but devoid of an epimatium.

(*b*) The epimatium forms an almost complete investment to the ovule, as in *Podocarpus*, but differs in being entirely fused with the integument, even in the region of the micropyle, in the formation of which it takes part. Thus, as in *Podocarpus*, the "outer flesh" of the seed consists peripherally of the epimatium and internally of the sarcotesta, an integral part of the integument.

The ovular stalk is here represented by the broad concave scale, of which the distal margin forms the curved ridge passing obliquely round the base of the seed. This ridge corresponds to the "apical knob" in *Podocarpus*. Except for the greater fusion of the epimatium *Acmopyle* is practically a *Podocarpus* with a semi-erect and highly vascular seed. So far as the epimatium is concerned the three genera form a linear series with *Podocarpus* in the middle.

The second view is preferable on all hands; it does not involve the assumption of any new morphological combination but fits in with the conditions already existing in *Podocarpus*, the differences being to a large extent traceable to the orientation of the seed. Moreover, the persistence with which the so-called "apical knob" (SINNOTT, 1913, p. 42) occurs both in *Dacrydium* and *Podocarpus* leads to the suspicion that it carries a deep morphological significance; and it is difficult to set aside the obvious similarity of the curved ridge on the back of the seed in *Acmopyle* to that described by Miss GIBBS in *P. vitiensis* (1912, fig. 14). This is no doubt the same structure which in *D. taxoides* (PILGER, 1903, p. 47, fig. 4),* in *D. falciforme* (GIBBS, 1914, p. 192, fig. 8) and in *P. andinus* (PILGER, 1903, p. 65, fig. 10) develops into a long horn-like process, especially in the young ovule, but which in *P. Nagi* and § *Eupodocarpus* is either reduced to an insignificant tip or is completely merged in the scale. There is no doubt, too, that this organ is the homologue of the distal end of the ovuliferous scale of other Conifers (see SINNOTT, 1913, p. 75).

### 2. *The Orientation of the Seed.*

With its erect seed *Acmopyle* clearly resembles *Dacrydium* rather than *Podocarpus*, and the question arises whether this feature has been retained from a *Dacrydium*-like ancestor, or whether it is a secondary acquirement.

In *Dacrydium* the final position of the ovule varies from the nearly erect (*D. Fonkii*, *D. laxifolium*, etc., see PILGER, 1903, p. 49, fig. 5) to the nearly

* As Miss GIBBS points out (1914, p. 192), PILGER'S figs., H-L, on p. 47 of his 'Monograph,' are erroneously referred to *D. falciforme*.

horizontal (*D. taxoides*, see PILGER, 1903, p. 47, fig. 4) while the completely inverted seed is confined to *Podocarpus*.* SINNOTT (1913, p. 71), who has propounded the reduction theory of Podocarpineæ, regards the inverted seed of *Podocarpus* as the more primitive condition, from which he derives the more erect seed of most species of *Dacrydium*. In accordance with this view he regards as a case of recapitulation the resemblance between the final stage of *Podocarpus* and the young stage of *D. colensoi* and *D. intermedium*, in which the ovule is inverted and the epimatium overtops the integument (SINNOTT, p. 49).†

However, it has long been known through the work of STRASBURGER (1872, Plate 2, figs. 39*ff*) and of BAILLON (1873, Plate 8) that the ovule of *Podocarpus chinensis* executes during development a movement in the opposite direction, namely, from a nearly horizontal to a completely inverted position. STILES (1912, p. 470) records a similar movement in *P. latifolius*, and Miss GIBBS' photograph (1912, fig. 79) of a comparatively young ovule of *P. elata* leads to the same conclusion.

These facts about *Podocarpus* are not here cited as reminiscences of a dacrydioid ancestry; but they at least indicate the uncertainty attending the interpretation of the juvenile stage of *Dacrydium*.

As regards the posture of the young ovule of *Acmopyle* a definite statement is naturally at present out of the question, but even if it is found to be inverted, it would be difficult to argue that the sub-erect position of the ripe seed is the expression of a dacrydioid affinity, for in the only other points in which *Acmopyle* departs from *Podocarpus* it does so in a direction opposite to that of *Dacrydium*. As already concluded above from a consideration of the epimatium the three genera probably form a linear series with *Podocarpus* in the middle; the nearly erect position of the seed of *Acmopyle* is therefore probably to be regarded as a recent secondary acquirement. If the reduction theory is to be maintained—a view to which I do not subscribe—*Acmopyle* must be the most primitive member of the family, both in view of the total fusion of the epimatium and of the great complexity of the entire female reproductive organs.

### 3. *The Vascular Structure of the Seed.*

This complexity is perhaps most clearly seen in the vascular supply of the seed, which is the best developed not only among the Podocarps but among all known Conifers.

* PILGER states that the three New Zealand species of *Dacrydium* (*D. Bidwillii*, *D. Kirkii*, *D. biforme*) have their seeds completely inverted, as in *Podocarpus*; they have for this reason been regarded as showing an interesting transition between the latter genus and the remaining species of *Dacrydium* (SINNOTT, 1913). I have, however, found evidence to show that *D. Bidwillii*, and probably also the other two species, belong properly to the genus *Podocarpus*, of which they would probably form a distinct section. (SAHNI, 1918A, p. 219.)

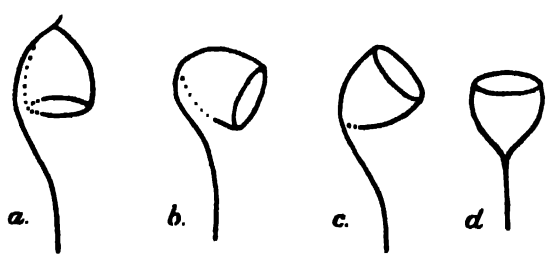
† The same inverted condition is seen in the young ovules of *D. cupressinum* (PILGER, 1903, p. 54, fig. 6), *D. taxoides* (PILGER, p. 47, fig. 4), and *D. falciforme* (GIBBS, 1914, p. 192, fig. 8); on the other hand, some young ovules of *D. laxifolium*, on which I hope soon to publish notes, are only slightly inclined from the erect position, the ripe ovules being perfectly erect.

Apart from the presence in *Acmopyle* of a more or less continuous vascular network (cupule) in place of the separate strands of *Podocarpus*—which is only a matter of degree of development—the differences in the distribution of the vascular supply in the two genera are no doubt to be traced chiefly to the different posture of the seed. This view is illustrated in text-fig. 38 by means of a series of purely diagrammatic sketches of the vascular skeleton. For the sake of simplicity, the descending portion of the ovular supply in *Podocarpus* (text-fig. 38, *a*) is also shown as a continuous vascular mantle, as in *Acmopyle* (text-fig. 38, *c*).

The series of diagrams may be read in either direction according to the view adopted as to the relative antiquity of the two genera. Assuming for the sake of argument, that the ovule of *Podocarpus* is more primitive than that of *Acmopyle*, as the ovule gradually erects itself, its ventral surface would become free from the "ovular stalk," and would thus be left with a gap in the vascular supply originally occupied by the ascending strands. We could then reasonably expect that the existing strands would tend to distribute themselves more evenly round the circumference of the ovule wherever the latter is free from the "stalk," so as to ensure a supply to the ventral side as well. This ventral completion of the vascular ring would begin at the micropylar end (which would be the first to become free) and gradually extend towards the chalaza as the ovule was tilted up. At an inclination of about 45° a condition would be reached not very unlike that actually seen in *Acmopyle*. It is now easy to see the significance of the fact—which at first was rather puzzling—that there is no direct connection, at the chalazal end of the seed of *Acmopyle*, between the strands on the ventral side and those on the dorsal (see p. 275 and text-fig. 20).

The next stage, shown in text-fig. 38, *d*, is hypothetical, and shows the presence of such a connection in the final phase of erection. The stage shown in text-fig. 38, *b*, is also hypothetical.

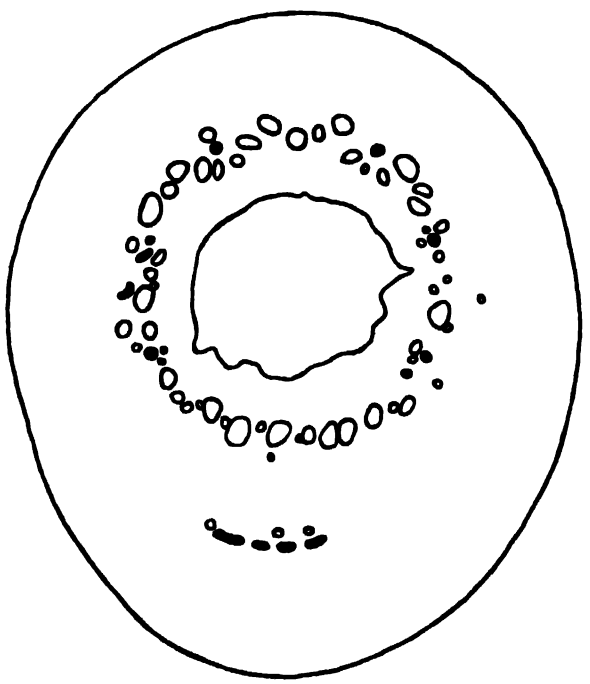
Arguing in the reverse direction—that is, if the seed of *Acmopyle* is regarded as more primitive than that of *Podocarpus*—one would expect that, as the ovule gradually became more and more inclined and its mid-ventral surface became fused to the "stalk," the vascular strands on that side would tend to become atrophied, for they would be superfluous in the proximity of the ascending strands of the "stalk." This atrophy would naturally begin at the chalazal end, and gradually work its way towards the micropyle.




TEXT-FIG. 38.—Diagrams. See text above.

If the above interpretation is correct, it is apparent that in *Podocarpus* the ascending and the descending strands do not properly belong to one and the same system, for the descending strands (which I think belong strictly to the integument, and not to the epimatium) represent a cup-like system pendent from the distal region of the ascending system.

It is of some interest to find a little confirmation of this view in the adjoining figure of *P. bracteata*, BLUME* (text-fig. 39). The section passed through a level about midway between the micropyle and the equator. It will be noticed that the ring of descending strands is incomplete on the "stalk" side, and, what is more important, that the line bridging the gap leaves the row of ascending strands an appreciable distance outside the ring.† The disposition of the mucilage canals, too, which form a complete circle of their own apart from the canals of the ascending strands, is probably not without significance. At a higher level the ascending strands approach the gap and finally themselves occupy the gap. A section from a level between the chalaza and the equator therefore gives the misleading impression that all the strands in the ring belong to the same system. (See STILES's fig. 4, *e*, *f*, p. 471, for *P. macrophyllus*, which will do equally well for the closely allied *P. bracteata*.)



TEXT-FIG. 39.—*Podocarpus bracteata*, BLUME. Transverse section of seed at a level midway between the micropyle and the equator. The vascular bundles are shown solid black.

* Synonymous with *P. neriifolius*, DON.

† I have observed the same feature in one other (unidentified) species of *Podocarpus* (§ *Eupodocarpus*), and consider it very probable that it occurs in several other species. The fact that STILES does not figure or describe the phenomenon in *P. macrophyllus*, a species closely allied to *P. bracteata*, may be due to his sections not having passed through the region to which this condition appears to be limited.

The conception of a cup-like vascular system pendent from the chalaza occurred to FAVRE (1865, p. 381) as early as 1865 from his study of *Podocarpus chinensis*, but, so far as I am aware, no one has followed up his suggestive idea.

In homologising the vascular system of the female organs of *Podocarpus* with that in *Acmopyle*, it must be recognised that what in *Podocarpus* is known as the "ovular stalk," adnate to the whole length of the seed and forming a distinct bulge in the transverse section, is in *Acmopyle* flattened out into a thin, curved lamina, so completely fused to the basi-dorsal surface of the seed that except for the curved ridge indicating its margin it would be impossible to detect its presence. The ascending strands of *Podocarpus* would correspond not only to the pair of large inverted basal strands in *Acmopyle*, here of very short length, but also to a portion of the dorsal valve of the cupule into which they distally expand. The distal limit of the "ascending system" of *Acmopyle* would probably be marked by the reflexed strands in text-fig. 26 which, as stated on p. 276, lie just under the ridge. That portion of the dorsal valve of the cupule which lies beyond the ridge would thus correspond to the "descending system" of *Podocarpus*. The ventral part of the cupule of *Acmopyle* must be regarded as a new acquisition, related in origin to the semi-erect position of the seed.

Although in broad outline, the above suggestion seems to afford a reasonable interpretation of *Acmopyle* in terms of *Podocarpus*, there remains one difficulty, which must at present remain unexplained, namely, the double nature of the cupule on the ventral side of the seed. Is it that the erection of the seed from the *Podocarpus*-like condition took place in two distinct stages, so that first the outer ventral arc was acquired and then the inner? The fact that of the two arcs the inner extends to a point nearer the chalaza (see text-fig. 6) than does the outer at any rate does not contradict this hypothesis. In this connection an examination of younger material would be of some interest On the other hand, it may of course be that the process of erection is not merely ontogenetic, but is spread over the phylogeny of *Acmopyle*. In that case a *Podocarpus*-like form must have existed with a horizontal seed intermediate between these two genera.

We shall now consider STILES's theory that the elaborate vascular system of the seed of *Podocarpus* is not homologous with that in the older Gymnosperms. As stated on a previous page, I prefer to draw the line between the integument and epimatium just outside the ring of descending strands, considering only the peripheral portion of the flesh as the epimatium, and the inner region (containing the descending strands) as an integral portion of the integument. STILES, on the other hand, draws the line at the outer limit of the stony layer (1912, p. 475, and figs. 6, 7), thus assigning the descending as well as the ascending strands to the epimatium, and implying the absence of a sarcotesta proper to the integument. If the broken line in the figures cited were, indeed, the limit between the integument and epimatium, it is clear that STILES's theory would follow as a corollary, for the

epimatium, being homologous with the ovuliferous scale, is not an integral part of the ovule; its vascular supply cannot therefore be homologised with that of the Cycads, which is strictly ovular.

Stiles, however, arrived at his conclusions by a different route. Arguing that the vascular system of the *Podocarpus* ovule is an elaboration of the rudimentary system in the more primitive members of the family, he concludes that the ovular system of the Podocarpeæ has been evolved within the family, and is therefore not homologous with that in the older Gymnosperms.

But I consider it possible that, during its evolutionary history, an organ may become much reduced, and subsequently attain a considerable development along different lines. Thus I regard the vascular system of the ovule of *Acmopyle* as homologous with that in the Cordaitalean ancestor, although in the modern genus the outer set of bundles has become well developed, while the inner has disappeared.

Unfortunately, the question is one that does not admit of a solution by positive histological evidence of any value. So far as I know, the descending strands have not been traced into the epimatium beyond its point of separation from the integument; on the other hand, it is equally true that they have not been traced into the free micropylar region of the integument.*

In the absence of direct evidence, therefore, we are left to whatever indirect evidence may be available from comparisons with other Gymnosperms. Perhaps the strongest argument against the theory advanced by Stiles lies in the fact that the seeds of the Podocarpineæ, and, in fact, of all the Conifers, conform to the fundamental plan of structure of the typical platyspermic seed, and that, for this reason, such an important difference as that involved in the theory would be a *primâ facie* improbability.

Thus, two basal main supply strands, situated in the right-left plane, are an invariable rule throughout the Podocarps, as they are in the Cordaitales, *Ginkgo*, and the Taxineæ. When there is an inner or an outer system of strands (or when both systems are present), the strands, if unbranched, always lie in the plane of the carinæ (right-left plane), in the Cordaitales, *Ginkgo*, the Taxineæ, and in the only Pinaceæ in which they have been recorded, viz., *Abies* and *Cedrus* (Radais, 1894, Plates 2 and 6). In those species of *Podocarpus* in which there are only two descending strands, *e.g.*, *P. ferrugineus* and the species commonly known as *Dacrydium Bidwillii*, these always lie in the plane of the carinæ, and in *P. ferrugineus* they are actually in contact with the latter (Sinnott, 1913, text-fig. 3, p. 46). In *Acmopyle*, too, it is significant that it is the carinal portions of the vascular cupule that reach nearest the micropyle.

* Miss Gibbs (1912) has given very useful figures of longitudinal sections of several species of *Podocarpus*, but from their diagrammatic character it is difficult to be sure of the correct positions of the strands. In any case they lie very near the limit. This author does not go into the question under discussion.

The correspondence, in the vascular organisation of the seed, between the Podocarpineæ and the remaining Gymnosperms, is so close that, unless there are strong reasons to the contrary, it is natural to recognise the homology of the different parts of the vascular system. It may therefore be concluded that the inner region of the fleshy seed-coat, which contains the "descending" strands, is really a part of the integument proper.

As regards the inter-relationships of the remaining genera of the Podocarpineæ, this subject has been admirably dealt with by STILES (1912, pp. 489–496), the main trend of whose argument appears to be convincing. I would only like to suggest that the genus *Dacrydium*, instead of forming a side line from *Microcachrys* (see the scheme on p. 496 of STILES's paper), may probably lie in a direct line, leading to *Podocarpus*, *Microcachrys* itself lying at the base of *Dacrydium*, as already indicated by STILES. It is rather surprising that, in the scheme proposed by STILES, *Dacrydium* does not appear as a link between *Microcachrys* and *Podocarpus*, for, from *Dacrydium Bidwillii* (as the plant was then known) to *Podocarpus*, the transition is so much more gradual than it is from *Saxegothæa* to *Podocarpus*.

Further, although I agree with STILES that *Saxegothæa* and *Pherosphæra* are two of the most primitive Podocarpineæ, I would not commit myself to any definite view as to their connections with the other genera of the family, especially as our knowledge of *Pherosphæra* is exceedingly meagre. The position of *Saxegothæa* is so clearly intermediate between the Podocarps and Araucarians (STILES, NORÉN, TISON, THOMSON) that it raises the question as to whether it would not be advisable to place this genus in a separate tribe, *Saxegothææ*, linking together the other two. It is significant that TISON (1909, p. 156) proposed the inclusion of *Saxegothæa* in the phylum Araucariales instituted by Prof. SEWARD and Miss FORD (1906, p. 398).

*Phyllocladus* appears to represent a branch leaving the main stem at about the level of *Dacrydium*, to which, apart from its specialised vegetative characters, it appears to show more resemblance than to any other Podocarp. The symmetrical nature of the epimatium would thus appear to have been secondarily acquired, for the ovule is erect throughout its development. Mrs. ARBER has already suggested that there is a correlation between the symmetry of the epimatium and the posture of the ovule.

### B. *The Systematic Position of the Taxineæ.*

We may enter now upon the wider question of the affinities of the Podocarpineæ to the other groups of Conifers and the ancestry of the Conifers themselves. Since the discussion is intimately bound up with the inevitable question of the morphology of the ovuliferous scale, it is advantageous to make the latter a starting point.

But before dealing with this subject it is necessary to point out that I have ventured to exclude from the phylum Coniferales the genera *Taxus*, *Cephalotaxus*, and *Torreya*. Both the general morphology and the internal structure of the fructifications lead me to the conclusion that the family Taxineæ is too distinct to occupy

a place among the Conifers, and that it should rank as an independent phylum, Taxales,* related to *Ginkgo*, to the Cordaitales, and to the Coniferales as here defined.

In LINDLEY'S 'Vegetable Kingdom' (1853, p. 231), the Order Taxaceæ, which included the Yews and Podocarps† as well as *Ginkgo*, appeared as a group of equal rank with the Cycadaceæ, Gnetaceæ, and Pinaceæ. The latter group was also named Coniferæ, a term which has since acquired a wider significance, for it now covers both the Pinaceæ and Taxaceæ of LINDLEY, with the exception of *Ginkgo*.

In the most up-to-date general work on Gymnosperms (COULTER and CHAMBERLAIN, 1917) these two groups appear as equivalent orders of the phylum Coniferales. However, as Dr. SCOTT (1911, p. 172) has remarked, "it is doubtful whether even this first grouping is natural, for the Podocarps among the Taxaceæ seem to have little to do with the Yews."

The opinion that the relation between the Yews and the Podocarps is not a close one dates at least as far back as 1838, when BENNETT and BROWN (1838, p. 36) wrote as follows: "It is singular that so unessential a character as the general solitary position of the ovuliferous scale should have induced all the authors who have attempted an arrangement of the Coniferæ to separate *Podocarpus* and *Dacrydium* from the true Pines and to associate them with the Yew." PILGER expressed exactly the same view in 1903 (pp. 25, 38). In 1910, BROOKS and STILES (p. 316) observed: "The points of similarity between the Podocarpeæ and the Taxeæ do not seem to us to be very striking;" and in 1912, STILES (498–499) wrote: "It is at least safe to say that there is as yet little evidence of any near connection of the Taxeæ and Podocarpeæ," at the same time enumerating several important structural features in which the two groups show a "marked contrast."

Remembering that LINDLEY was unaware of the presence of motile sperms in *Ginkgo*, his placing that genus in relation to *Taxus*, *Cephalotaxus*, and *Torreya* may be regarded as a natural step; but in including *Dacrydium* and *Podocarpus* in the same Order as *Taxus*, he was probably unduly impressed by the tendency in all these genera towards a fleshy development of some parts of the female fructification, which may not necessarily be homologous. The Yew berries, for example, closely resemble the dry seed of *Dacrydium laxifolium* perched upon the delicate fleshy receptacle composed of swollen bract bases.

In 1906, Mrs. AGNES ARBER (Miss ROBERTSON, 1906, p. 101), expressed the opinion that "the general morphology of the female 'flower' of *Taxus* more closely recalls that of *Cordaites* than that of any other known plant." At the same time *Ginkgo*, itself showing strong Cordaitean features, has long been known as an ally of *Cephalotaxus*—an alliance which, as Dr. SCOTT observes (1906, p. 143), was

* A name previously employed by LOTSY (1911, p. 160), but not in the sense of a group equal in rank with the Coniferales.

† With the exception of *Pherosphæra*, *Saxegothæa*, and *Microcachrys*. In his 'Natural System' too (1836, p. 317) LINDLEY had associated *Taxus* with the genera *Podocarpus*, *Dacrydium*, *Phyllocladus*, and *Ginkgo*.

established before the discovery of the motile sperms. If we agree with Dr. SCOTT that the Yews have little to do with the Podocarps, it may confidently be added that they have still less to do with any other Conifers.

Had it not been for the genus *Phyllocladus* which chiefly on account of its symmetrical epimatium, appears to link the remaining Podocarps with the genus *Taxus*, it is extremely probable that the Order Taxaceæ would not so long have preserved its integrity. It is, therefore, of importance critically to examine the evidence upon which *Phyllocladus* claims a Taxinean affinity.*

It is noteworthy that with the exception of PILGER, who placed *Phyllocladus* in a tribe intermediate between the Taxineæ and Podocarpineæ, nearly all the modern writers on the subject have definitely expressed the view that the affinities of the genus are clearly with the Podocarps, and have considered it unnecessary to retain the intermediate tribe (KILDAHL, 1908, p. 465; YOUNG, 1910, p. 91; BROOKS and STILES, 1910, p. 316; STILES, 1911, p. 346; STILES, 1912, p. 445).

Mrs. AGNES ARBER (Miss ROBERTSON, 1906)—who was the first to investigate this interesting genus in detail—while fundamentally agreeing with this view, appears to have been impressed, rather more than the other authors, by certain features in which *Phyllocladus* seemed to approach the Taxineæ rather than the Podocarpineæ. However, at the time when Mrs. ARBER wrote her lucid paper on *Phyllocladus* our knowledge of the Podocarpineæ was very meagre: in the light of facts which have since been observed, out of the few characters which were then suggested as being Taxinean rather than Podocarpean, all except one appear to lose much of their value.

(i) *Presence of Centripetal Wood in the Cladodes.*— Mrs. ARBER herself does not lay much stress on this point, and I think justly. It is still a moot point whether transfusion tracheides found in the vicinity of the protoxylem, and often separated from it by parenchyma, should be reckoned as true centripetal xylem. But whatever view be adopted on this point, the tissue referred to in *Phyllocladus* is found in numerous other Conifers (including *Dacrydium*, *Podocarpus*, *Acmopyle*) in exactly the same relative position, and without leaving any doubt as to its identity with it.

Although in *Phyllocladus alpinus* Mrs. ARBER records the presence of this tissue only in the lateral bundles of the cladode, in my preparations of *P. asplenifolius* and *P. trichomanoides* (the latter closely allied to *P. alpinus*) it occurs not only in all the strands of the branch-system of the cladode, but also in the scale-like leaves of the unmodified shoot.

* In all the following features it differs from the Taxineæ, while at the same time resembling the Podocarps:—The form and structure of the male cones and stamens; winged pollen; male gametophyte; the general morphology of the female cone with each ovule always clearly subtended by a bract; free nucellus (entirely absent in the Taxineæ, but present in some Podocarps); presence of spongy tissue and a thick two-layered megaspore-membrane (a feature of doubtful value; although conspicuously absent in the Taxineæ it is also absent in some Podocarps); general vegetative anatomy, such as the presence of root tubercules and entire absence of bar thickenings in the secondary wood; and, finally, the southern distribution of the genus (the Taxineæ being chiefly northern forms, the Podocarpineæ chiefly southern).

(ii) *Taxinean Sculpturing.*—Mrs. ARBER discovered that the tissue just referred to, for which I prefer the non-committal name of transfusion tracheides, showed in *Phyllocladus* a peculiar type of sculpturing, which combined small scattered narrowly bordered pits with band-shaped thickenings; the latter passed round the cells in various directions, specially when the cells were iso-diametric. A rather similar type of ornamentation was recorded in the "normal" xylem. By the latter term I understand that only the primary xylem is meant; for in the two species examined by me (one of which, as already stated, is very similar to *P. alpinus*) I could not discover any trace of band-like thickenings in the secondary wood, and it would be surprising if these were found in *P. alpinus.**

It is doubtful whether we can justly refer to this feature as true Taxinean sculpturing, which is rather different in appearance and *is always present in the secondary wood.* Moreover, it is important to mention that I have observed exactly the same type of tracheides as those recorded in *Phyllocladus*, in the primary xylem of *Acmopyle* (see text-fig. 1), in two species of *Podocarpus* and in *Dacrydium laxifolium.* In none of the members of this family, however, does the secondary wood show any band-like thickenings at all.

(iii) *The Erect Posture of the Seed.*—As Mrs. ARBER herself states, a nearly erect seed is also found in *Dacrydium laxifolium*† and, we may add, on the authority of PILGER, in *D. Fonkii*, *D. Franklinii* and, of course, *Acmopyle.* In some ripe material of *D. laxifolium* and *D. cupressinum* examined by me the seeds are perfectly erect; the same condition is figured by KIRK in *D. intermedium* (1889, Plate 87B), and also in the two former species.

However, the seed is in these cases not erect in the same sense as in *Taxus* where the nucellus is evidently from the very outset the direct continuation of the seminiferous axis. The condition in *Taxus* is more readily compared with *Cordaites* and *Ginkgo* than with any of the Podocarps.

(iv) *The Symmetrical Epimatium.*—It cannot be denied that this character is more Taxinean than Podocarpean, but there appears to be some reason for the view that the symmetry of the epimatium of *Phyllocladus* has been secondarily acquired (see above, p. 287). This feature, as suggested by Mrs. ARBER, is probably correlated with the erect position of the seed, exception being made, of course, in those cases where an inclined ovule with an asymmetrical epimatium subsequently becomes erect, as in *Dacrydium.* In *Acmopyle*, too, the epimatium is symmetrical, at least in the major portion of the seed—a fact which, by the way, would seem to suggest that the young stage of the ovule is probably not much more inclined than the ripe seed, or at least not completely inverted.

* Since the above was written I have been able to confirm their absence in this species from Mrs. ARBER'S original preparations, which she most generously placed at my disposal for comparison.

† The spelling of the specific name as "latifolium," repeated by Miss KILDAHL (1908, p. 465) is evidently a misprint.

Mrs. ARBER justly observed that it would not do to lay too much stress upon the usually asymmetric nature of the epimatium of the Podocarpeæ, as showing that this organ is not homologous with the aril of *Taxus* and *Torreya*. At the same time, the symmetrical epimatium of *Phyllocladus* and *Acmopyle* does not necessarily indicate a homology with the aril of *Taxus*, for any extra seed-coat would tend to develop symmetrically if subjected to uniform surroundings, such as obtain in the case of erect ovules. It would seem, therefore, that the symmetry of the epimatium of *Phyllocladus* speaks neither definitely for nor against its homology with the aril of *Taxus*.

The Taxales stand apart from the Coniferales in the general organisation of their ovuliferous shoots and in the retention of obviously primitive characters in the seed (OLIVER and CHICK, 1902; OLIVER, 1902) and seedling (CHICK, 1903). They are the only living Gymnosperms which, having relinquished the zoidiogamic mode of fertilisation, still linger behind the others in preserving the vanishing traces of an internal vascular system in the seed (OLIVER, 1903). The male cones are very distinct from those of the Conifers, especially in the habit and in the frequent presence of bracts between the groups of stamens. The importance of the presence of bracts (*cf.* Cordaitales) is probably very great. The individual stamen, too, is in *Taxus* totally unlike that in any Conifer, although in *Torreya* there are unmistakable signs of progress in that direction by a gradual departure from the peltate form. In spite of this, however, the mode of insertion and general appearance of the branched bracteate male cone of *Cephalotaxus* remains strikingly different from that of any known Conifer.

The entire absence of vegetative prothallial cells in the male gametophyte may also be reckoned as a feature of some importance in distinguishing the Taxales, for although it is found also in the Taxodineæ and Cupressineæ, these two tribes are in most other respects so markedly different from the Yews that this resemblance can hardly be traced to a near relationship. A similar argument applies to the so-called "taxinean sculpturing" in the secondary wood, for it occurs in some of the Abietineæ (*Pseudotsuga*, *Larix*, *Picea*; see GOTHAN, 1905, p. 98) —a tribe of Conifers which probably has very little to do with the Taxales.

It is difficult to say what significance can be attached to ROTHERT'S discovery of so-called "parenchymatous tracheides" in the pith of a species (or perhaps only a variety) of *Cephalotaxus* (1899, p. 275). From ROTHERT'S account and from some preparations which Mrs. ARBER very kindly allowed me to examine, these tracheides do not essentially differ from the familiar transfusion tracheides associated with the leaf-strand in numerous Conifers. In their presence in an axial organ they are certainly unusual, but not unique, for similar elements occur also in the branch system of the cladode of *Phyllocladus* (see p. 289). Mention may also be made of the fact that the presence of secretory canals in the pith of the stem—a very uncommon feature in which the genera *Ginkgo* and *Cephalotaxus* agree—has been emphasised by VAN TIEGHEM (1891A, p. 189), as a sign of affinity.

The position adopted by several writers, such as R. B. THOMSON (1905, pp. 45 and 54), LAWSON (1907, p. 20), COULTER and CHAMBERLAIN (1917, p. 418), and BLISS (1918, p. 56), that the Yews represent a relatively modern group, appears to be untenable in view of the evidence from the morphology of the male and female organs, specially the presence of bracts in the male cone and the structure of the seed.

The absence of a thick megaspore membrane has been employed by Prof. THOMSON (1905) in support of the view that the Taxineæ are a recent group. This author examined *Taxus canadensis* and states (p. 45): "The later stages of *Taxus* up to maturity of the seed gave no indication of the presence of a megaspore-coat." However, in *T. baccata* a species closely allied to, if not identical with *T. canadensis*, I found that, although the megaspore membrane is really a "negligible feature" at the early free-nuclear stage of the prothallus, at the time of embryo formation it is of appreciable thickness. While the thick membrane of the Cycads and *Ginkgo* is thoroughly in accord with their primitive nature, the value of this criterion in the other groups is still doubtful, specially in the Podocarpineæ, among which both thick and thin megaspore membranes occur. In particular I may mention that in my preparations this variation is even seen within the genus *Podocarpus*, which, so far as I am aware, has hitherto been known only to have a poorly developed membrane, in contrast to *Dacrydium*. Thus the two species of *Podocarpus* hitherto known as *Dacrydium Bidwillii* and *D. Kirkii* (see p. 282, footnote*), as well as *Podocarpus alpinus* (§ *Eupodocarpus*) have each a well-developed megaspore membrane like that of *Dacrydium* or *Phyllocladus* (ROBERTSON, 1906). One other species belonging to § *Eupodocarpus* shows a medium thickness.

Prof. OLIVER'S work has conclusively shown that *Torreya* possesses one of the most primitively organised seeds among living Gymnosperms. From his study of the seed of *Cephalotaxus*, WORSDELL (1900, pp. 317–18) has come to a similar conclusion with regard to this genus. The resemblance in the general morphology of the female shoot of *Taxus* and *Cordaites* has also been widely recognised. These considerations impelled me to search for possible archaic features in the mature seed of *Taxus*, and to attempt to describe it in terms of *Torreya*, which, according to Prof. OLIVER'S well-known theory, is not difficult to derive from a type like *Cardiocarpus*. The result of this search has been to convince me that the seed of *Taxus* is in some respects even more primitive than that of *Torreya*, appearing, in fact, to form the terminal link in a remarkable chain of seed-types, leading from *Cardiocarpus* through *Cycadinocarpus*, *Rhabdospermum*, *Mitrospermum*, and *Taxospermum*, to the living genus *Taxus*.

It would take us too far here to discuss the relations between the different stages of this series, which, although not by any means suggested as representing the actual course of evolution, yet appears to illustrate progression along certain well-marked tendencies, which would seem to bridge up the structural gap between the seeds of

the Cordaitales and those of the Taxales. I hope shortly to deal with this subject in a separate paper.*

### C. *The Ovuliferous Scale of Conifers.*

In the entire domain of plant morphology, there is no structure which has exercised so wide an influence upon our views on the phylogeny of a group as the ovuliferous scale of Conifers. Out of the mass of literature, dating from nearly a hundred years ago, two rival theories stand out prominently: (1) the Brachyblast Theory; (2) the Ligular Theory.

The question is so wide, and has so often been handled by experts, that I cannot pretend to deal with the entire evidence. I shall, however, venture to go into some detail with regard to the evidence from the vascular anatomy, which, I may say beforehand, appears to me to be conclusively in favour of the Brachyblast Theory.

(a) *Evidence from Vascular Anatomy.*—The most striking fact that emerges from a general survey of the literature† is that, at its origin, the supply to the ovuliferous scale is fundamentally similar to that to a vegetative axillary branch, while sometimes the resemblance is so close that a distinction appears impossible. The similarity between the vascular supplies of the ovuliferous scale and vegetative axillary bud was frequently urged by STRASBURGER in his classical work on the Conifers and Gnetaceæ (1872, frequent statements scattered over pp. 25–75, in connection with *Biota*, *Juniperus*, *Araucaria*, *Agathis*). More recently, EAMES (1913, p. 21) has laid emphasis on the same feature. But no author has illustrated this point so clearly as Miss AASE (1915) has quite recently done in a detailed paper on the vascular anatomy of the megastrobili of Conifers. A comparison of her figures, specially of *Pinus maritima* and *P. Banksiana* (pp. 286, 287), besides numerous others, is alone sufficient to demonstrate the identity of the vascular relations; in both the ovuliferous scale and the vegetative axillary bud the supply comes off typically from the sides of the foliar gap in the axial cylinder.

The vascular structure of *Acmopyle*, too, shows the fundamental similarity between the supply to the ovuliferous scale (or its vestige) and the vegetative axillary shoot (see above, pp. 267, 268, and text-figs. 5, 7–18). In this connection, a comparison of text-figs. 5 and 10 of the present paper with Mrs. ARBER'S (Miss ROBERTSON'S) figure of the vegetative stem of *Phyllocladus* (ROBERTSON, 1906, Plate 17, fig. 7) and STRASBURGER'S figure of *Sciadopitys* (1872, Plate 26, fig. 5) is particularly illuminating.

From such data as these, the axial nature of the ovuliferous scale appears to be clearly demonstrated.

Soon after its origin, the supply to the scale becomes arranged in the form of an

* This paper has, since the above was written, been published in the 'Annals of Botany,' vol. 34, pp. 117–133, January, 1920.

† See especially the extensive researches of VAN TIEGHEM (1869), STRASBURGER (1872), RADAIS (1894), AASE (1915).

arc, having an orientation inverse to that of the subtending bract-trace.* This inverse orientation of the vascular supply, while being intelligible on the brachyblast view, is an obstacle in the way of the ligular theory. EICHLER (1881, p. 1026) states that the inverted orientation is a property of the supply to all excrescences of the leaf, whether they come off from the upper or from the lower face, but it is doubtful if this statement is at all of general application. It fails, as EAMES has already pointed out, in the irregular orientation (most often concentric) of the ovular strands in many of the Conifers studied by RADAIS (1894, p. 286; see especially his figures of *Abies*, *Tsuga*, and *Sciadopitys*). Miss AASE (1915, p. 287) also records concentric ovular supply strands in *Ketcleeria Fortunei*. Since EAMES has already dealt with THOMSON'S (1909) statement relating to the alleged two inversions (one for the ovuliferous scale and one for the ovules), I will here only express my complete agreement with the former author.

As already noticed, in the majority of the cases on record, the ovuliferous scale supply showed a striking agreement with the supply to a vegetative axillary bud; it had an independent origin from the sides of the gap in the cone-axis cylinder. In other (comparatively few) instances the ovuliferous scale supply was described as branching off from the bract supply, and these instances have been employed in support of the ligular theory. Until recently, except for one or two genera, such as *Araucaria* and *Microcachrys*, there were no cases on record in which both these modes of origin were known in the same genus, nor was it generally realised that the relative sizes of the two parts of the cone-scale are subject to considerable variation, even in different regions of the same cone.

Thus THOMSON (1909) was led to believe that while in the Abietineæ (and, by inference, in the Taxodineæ and Cupressineæ) the cone-scale was evidently a double structure and the ovuliferous organ a modified axillary shoot, in the Araucarineæ and Taxaceæ (incl. Taxineæ and Podocarpineæ) the scale was simple, and the ligule of *Araucaria* and the epimatium of *Podocarpus* were mere excrescences of the upper surface. He thus founded two great groups of Conifers, the Diplosporophyllous and the Aplosporophyllous forms. This step has appropriately been criticised by EAMES (1913, p. 33).

More recently, Miss AASE (1915) has published facts which are of value in this connection, showing that the classification proposed by THOMSON is not tenable. A glance at her fig. 1, p. 283, will show that, according to THOMSON'S classification, the scales in the proximal region of the cone are aplosporophyllous, while those higher up in the same cone are diplosporophyllous. In *Pinus maritima*, *P. Banksiana*, *Ketcleeria fortunei*, *Cupressus Benthamii* Miss AASE describes both types of vascular

* The vascular cylinder of the brachyblast is to be conceived of as having a gap opposite to the subtending bract, as is usually the case with the vascular cylinder of the vegetative axillary shoot in its basal region, not only in the Conifers but also in many Ferns. If the ovuliferous scale is really a branch, it is evident that, strictly speaking, there is no sense in describing, as inverted, the strands on the side opposite to that on which the bract is placed.

supply (independent and joint) in different parts of the same cone. After reading her paper, I found the same feature in *Pinus silvestris*; I have also described it above in *Acmopyle* ('Vascular Anatomy of Receptacle,' p. 265 *ff*).

It is interesting to remark that almost all the different vascular relations between the ovuliferous scale and bract of Conifers are paralleled among the Ferns by those of the axillary branch and its subtending leaf; the analogy is indeed so close that the condition in the Ferns may throw light upon the morphology of the ovuliferous scale in Conifers. Those cases among Conifers in which the scale supply appears to originate partly or entirely in the trace of the subtending bract are analogous to the condition in the Hymenophyllaceæ and numerous other Ferns, in which the branch (whether adaxial or abaxial to the associated leaf) may be adnate to the petiolar base for a variable distance. In such cases it is entirely out of the question to regard the branch as an outgrowth of the leaf. As pointed out elsewhere (Sahni, 1917, p. 19), the basal undivided portion of the vascular supply must be regarded as having a dual nature, partly axial, partly foliar. Strasburger (1872, p. 69) has also drawn attention to somewhat similar analogies among Angiosperms, of which the adnate inflorescence of *Tilia* affords the most familiar instance.

The fact that the supply to the ovuliferous scale appears to arise from the supply to the bract, therefore, does not necessarily indicate that the one organ is morphologically an excrescence of the other.

(b) *Degree of Development of the Ovuliferous Scale as an Index of Affinities.*—Considerable importance has been attached by several authors to the degree of development of the ovuliferous scale as an index of affinity or of relative antiquity. While the exponents of the ligular theory have naturally interpreted the poorly developed ovuliferous scale of *Araucaria* and *Agathis* as signifying primitiveness, Prof. Jeffrey and his pupils, who believe in the brachyblast theory and in the Abietineous origin of the Conifers, have made use of the fact that in *Pinus* and allied genera the ovuliferous scale (in the middle region of the cone) appears more nearly to resemble an axillary shoot than it does in *Araucaria*. Finally, against those who advocate a Cordaitean ancestry for the Conifers, the criticism has been made (Seward and Ford, 1906, p. 393) that as we pass backwards in geological time we do not find an increasing development of the ovuliferous scale, which would bring the older Conifers (Araucarineæ) more nearly into line with *Cordaites*.

We have seen, however, that the degree of development of the ovuliferous scale is variable, not only within narrow circles of affinity (Eames, 1913, on *Athrotaxis* spp.), but even in different regions of the same cone (Aase, 1915). Keeping in view the analogy with the Ferns, where, as we know, the relative development of the branch and its associated leaf does not bear any definite relation to the systematic position of the plant, one is naturally inclined to ask whether even among the Conifers too much importance has not been attached to the degree of development of the ovuliferous scale as an index of relative primitiveness.

### D. *The Ancestry of the Conifers.*

(a) *Relative Antiquity of Abietineæ and Araucarineæ.*—If we exclude the Taxineæ, as suggested in this paper, there remain two groups, the Abietineæ and the Araucarineæ which, respectively, according to two rival schools of thought, claim to be the oldest living Conifers. It would be superfluous to repeat the evidence adduced by the two sides—both claim the support of the fossil record as well as that of the structure of living plants, and the controversy is certainly a beautiful example of the way in which practically the same data can be construed in diametrically opposite directions.

While the palæontological evidence (SEWARD and FORD, 1906) places beyond doubt the existence of Araucarians in the Palæozoic, the existence of Carboniferous and Permian Abietineæ has been shown to be without any proof. Of two fossil woods supposed by JEFFREY and CHRYSLER (1906) to belong to Palæozoic Abieteneæ, one has been shown to be not Abietineous and the other is equally certainly not Palæozoic. THOMSON and ALLIN (1912) have clearly demonstrated that the supposed horizontal resin-canals of the wood named by PENHALLOW *Pityoxylon chasense* (from the Permian of Kansas) are really the persistent leaf-traces of a *Dadoxylon* devoid of annual rings. The other wood, *Pinites Conwentzianus*, Goepp., the Abietineous nature of which Prof. SEWARD has confirmed by an examination of the original sections, was believed by GOEPPERT to be of Carboniferous age. The fossil was, however, found on a rubbish-heap, so that its correct age is extremely doubtful, and Prof. SEWARD has recently obtained further confirmation of this doubt (SEWARD, 1919, p. 220).

Both from the structural and from the historical side, the balance of evidence is at present decidedly in favour of the Araucarineæ being the more primitive group, and the resemblances which the latter group shows to the Cordaitales (BURLINGAME, 1915) are in accord with the view that they are more primitive than the Abietineæ. However, the facts at our disposal do not appear definitely to indicate that the one group is necessarily derived from the other. An independent origin from a common source is, at any rate, a safe hypothesis.

(b) *Fossil Podocarpineæ.*—Unfortunately, the fossil history of the Podocarpineæ—the family with which we are here more intimately concerned—is very imperfectly known. This is probably because, as BURLINGAME has hinted (1908, p. 175), "we know but little of the plant-remains of those parts of the world in which their remains would be most likely to be found." The probability of a relation with the Araucarians justifies the hope that undoubted Podocarpineæ may be discovered in the Mesozoic rocks, but it is for the future to show whether this group can at all rival in age the Araucarineæ.

Apart from abundant petrified wood of the *Podocarpus* type, numerous impressions have provisionally been referred to the Podocarpineæ.* Of these impressions, one

* The literature has been well summarised by STILES (1912, pp. 486–89); a more complete account is given in the fourth volume of Prof. SEWARD'S 'Fossil Plants.'

of the oldest, and also the most interesting, is the Rhaetic genus *Stachyotaxus*, NATHORST (1908, p. 11, Plates 2, 3), whose correct systematic position it is of great importance to ascertain, for it may, as hinted by Prof. NATHORST (p. 15, footnote), form a link between the Cycadophyta and the Conifers. The resemblance of this genus to *Cephalotaxus* is perhaps, on the whole, more striking than that to *Dacrydium*, in view of the paired ovules, symmetrical cup at the base, and the biseriately arranged leaves. But, as Prof. NATHORST says (*loc. cit.*, p. 15), the habit of the vegetative shoot is strikingly suggestive of *Podocarpus imbricatus*.*

The large two-winged pollen-grains discovered by Prof. NATHORST (1908, Plate 2, figs. 53–55) in the Triassic rocks of Sweden, and compared with pine-pollen, may equally well belong to extinct Podocarpineæ, for we are at present without any knowledge as to the contents.

A passing reference was made on a preceding page to a faint resemblance between the sculpturing of the sclerotesta of *Acmopyle* and that of the Palæozoic seed *Stephanospermum caryoides*, Oliver. Although this can only be regarded as a distant analogy, it was considered worth while to give detailed figures of the stone of *Acmopyle*, in view of the possibility that seeds with a similar pattern may be discovered in a fossil condition from the southern hemisphere.

It is also difficult to say what justification there may be for homologising with the "tent-pole" of *Ginkgo* and *Cordaites* the cone-like projection at the apex of the female prothallus of *Acmopyle* (see text-fig. 6). In order to see how far this feature is repeated in other members of the family, a search was made of the few published figures, showing the apex of the female gametophyte. Miss GIBBS (1912, Plate 49, fig. 6) figures a distinctly pointed apex in *Podocarpus imbricatus*. Miss YOUNG'S figure of *Phyllocladus* (1910, Plate 6, fig. 36) shows a condition particularly suggestive of *Ginkgo* and *Cordaites*, for there is a distinct central projection, surrounded by what looks like a deep trough, into which the archegonia open, but, in the absence of figures of transverse sections, I am unable to say if the archegonial depressions pass completely round the central peg.

(c) *Ultimate Origin of Conifers as a Whole.*—Whether the Conifers arose ultimately from megaphyllous (Pteropsid) or microphyllous (Lycopsid) ancestors is a question which cannot yet be regarded as settled, although it has engaged the attention of a number of eminent botanists for many years.† The more closely one tries to examine the evidence, the more distant does the solution appear to become, and I find it impossible to express a definite opinion. It goes without saying, that our knowledge of the older vegetations of the world is yet far from satisfactory; in the Devonian, or, it may be, in even older rocks, probably still lies buried the

* The figures (NATHORST, 1908, plate 2, figs. 19–24) also make it probable that *Stachyotaxus elegans* at least shares with *P. imbricatus*, *Acmopyle*, and *Dacrydium falciforme*, etc., the peculiar laterally compressed leaf-blade, for there appears to be no twist in the leaf-base.

† The discussion has recently been well summarised by BURLINGAME (1915).

answer to the question: Is the division of vascular plants into Pteropsida and Lycopsida so fundamental that it existed at their very origin from the non-vascular plants, or was the one class derived from the other? Naturally, if the megaphyllous forms have ultimately originated from microphyllous ones, the apparently divergent views as to the origin of the Conifers can to some extent be reconciled with each other. Thus, I believe it may be stated with confidence that the relatively near ancestors of the Conifers were forms like the Cordaitales. But the possibility of a remote Lycopsid connection,* without the intervention of true ferns or fern-like seed-plants, may not perhaps be entirely excluded, although at present there does not appear to be much evidence of a positive nature in support of such a connection.

As is well known, Dr. Scott (1909, pp. 650–652) has emphasised certain points of resemblance between the Cordaiteæ and the Pteridosperms, in support of the conclusion already expressed by him in 1902 (Scott, 1902) that the Cordaiteæ sprang from a Pteridosperm stock. In the first place, the seed in the two groups is constructed on the same general plan; secondly, by a gradual loss of centripetal xylem the stem anatomy of certain Pteridosperms passes into that of the typical Cordaiteæ. A number of Cordaitean stems are also known which approach the Pteridosperms in the possession of centripetal wood. In recent years the evidence for such an anatomical transition in the stem has been steadily increasing, and to express their intermediate structure, some of these Cordaitean stems were grouped by Scott and Maslen (1910) under the genus *Mesoxylon*, of which several species have now been described (Scott, 1912, 1918, 1919; Maslen, 1911).

So far as present knowledge goes, the Pteridosperms undoubtedly represent the nearest approach to the hypothetical ancestors of the Cordaitales. At the same time, there are important points of difference between the two groups, which have, of course, been recognised by Dr. Scott, but which may perhaps deserve as much emphasis as he has justly laid upon the resemblances. I wish to guard against the impression that I consider an origin of the Cordaitales from a Pteridosperm stock as improbable, but the wide differences between the two phyla, at any rate as we know them at present, do not readily fall in with this view.

* Naturally, an affinity so remote as may here be implied can hardly be expected to find expression in detailed structural resemblances: as may be inferred from my above-expressed belief in the brachyblast theory of the ovuliferous scale of Conifers, I do not agree with Schumann (1903, p. 71) in regarding the ligule of the Heterosporous Lycopods as being homologous with the organ so named in *Araucaria*. If such a homology existed, it might be reasonable to expect that the latter genus should preserve a trace of the ligule on the microsporophyll as well, if not on the vegetative leaf, in order to materialise the comparison with the Heterosporous Lycopodiales, which are never devoid of a ligule, even in the vegetative leaves. Schumann (1903, p. 70), who believes in the Lycopod origin of all Conifers, is so deeply impressed by the resemblances between the *Lepidocarpon* and the ovuliferous organ of the Conifers, that he considers it by no means certain that the Lepidodendreæ have correctly been assigned to the Pteridophyta. But the ligule of the Heterosporous Lycopods appears still to be a morphological enigma.

A review of the entire Gymnospermous series shows that there are two great divisions, based primarily upon the manner in which the seed is borne, whether upon the leaf or directly upon the axis. In the Pteridosperms and Cycads the seeds are always clearly borne upon the leaves, while in the Cordaitales (so far as known) and in the Ginkgoales, Taxales, and Coniferales they are borne either clearly upon an axis, or upon a structure which is probably some modification of an axis.* This differentiation of the Gymnosperms into two divisions, which I here propose to refer to as the Phyllosperms (with leaf-borne seeds) and Stachyosperms (with stem-borne seeds), respectively, appears to be very old, for, as far as I am aware, there is among the Pteridosperms no sign of a transition from the phyllospermic to the stachyospermic condition: a sharp differentiation is seen as far back as the available fossil records can take us. There could scarcely be a greater contrast in this respect than there is between RENAULT'S well-known figure of *Cordaianthus Williamsoni* (see SCOTT, 1909, p. 540) and the equally familiar figure of *Lyginopteris Oldhamia*, which forms the frontispiece of Dr. SCOTT'S 'Studies.'

Combined with this fact there are other important features, in which, as Dr. SCOTT points out (1909, p. 650), the Cordaiteæ and the fern-like seed-plants are as far apart as two groups of Gymnosperms very well can be. The strap-shaped parallel-veined leaves of *Cordaites*, and in fact the leaves of any known Stachyosperm, living or fossil, are entirely different from the much-divided fern-like fronds of the Pteridosperms or the almost equally complex leaves of the Cycads. The result is that in habit the two groups are totally distinct, and it is not easy to picture a Pteridosperm frond reduced into the simple Cordaitean leaf—at any rate, no intermediate form is yet known. Our knowledge of Cordaitean and Pteridosperm leaves is by no means complete, and transitional forms may yet be discovered; but until these are forthcoming it seems necessary to give due importance to the sharp contrast between the two types.

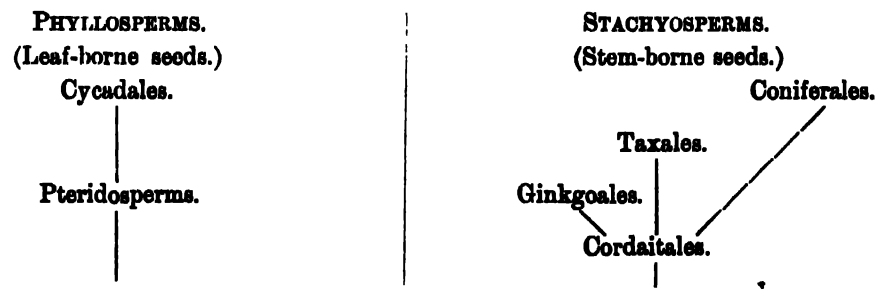
It is difficult to say whether we can extend to *Cordaites* the so-called phyllode theory of the leaf, originally applied to the monocotyledonous leaf. According to this theory, the typical monocotyledonous leaf represents only the proximal non-laminated region of the typical dicotyledonous leaf. Quite recently Mrs. AGNES ARBER (1918, p. 472) has published a paper of unusual interest, in which she brings forward convincing anatomical evidence which I think places the theory upon a firm basis, so far as the monocotyledons are concerned. In the leaves of *Cordaites* and the Conifers, however, similar anatomical evidence appears to be lacking. Nevertheless, I

* The importance of this difference between the Cycads and the Conifers was emphasised by STRASBURGER as long ago as 1879 (p. 139). As to the Gnetales and Bennettitales, further investigation is needed to show clearly whether they belong to the first category or to the second. STRASBURGER placed the Gnetales among the former class. On the other hand, in view of the far-reaching resemblances, in vegetative characters, of the Bennettitales with the Cycadales, the rather sharp contrast in the reproductive organs is disconcerting. The view has, however, been expressed (SEWARD, 1917, p. 382) that the seed-bearing pedicels of the Bennettitales are morphologically of a foliar nature.

consider it likely that the cupressoid type of leaf may have been produced by reduction from a taxoid leaf, and the latter from the multinerved type found in *Cordaites*, particularly as leaves similar to that of *Cordaites* also occur in the Araucarineæ. But the difficulty appears to lie in deriving the Cordaitean or Araucarian leaf from the much-divided fern-like frond, and this, it will be agreed, is the crux of the question. It is gratifying to learn that Mrs. ARBER hopes to return to this aspect of the phyllode theory, and her results may be awaited with interest, for light may be thrown upon the important question as to whether the apparent microphylly of the Conifers is due to reduction from a Pteridosperm-like condition or a reduction merely within the Conifers.

In the male organs, too, there is no clear resemblance between the Cordaitales and the Pteridosperms, the latter, as Dr. SCOTT points out, having no definite "cones." There appears to be hardly a comparison—except a rather distant one in form—between the "epaulets" of *Crossotheca* and the "stamens" of *Cordaites*. The one represents a minute portion of a dissected leaf; the other, according to the view which appears the most plausible, is itself an entire foliar organ, attached directly to the axis.* Each "epaulet" of *Crossotheca* may possibly be compared to a sorus on the microsporophyll of a Cycad, but not with the "stamen" of *Cordaites*; the latter organ is probably homologous with the microsporophyll of the Taxales, in which group the presence of interstitial sterile bracts in the male cone (*Cephalotaxus*) may considerably enhance the resemblance with *Cordaites*.

If the Stachyosperms and the Phyllosperms have had a common origin from megaphyllous ancestors it is clear that we must await the discovery of forms which show a transition from the leaf-borne to the stem-borne seed, as well as a reduction of the much-divided fern-like frond to the simple leaf invariably found in the Stachyosperms. A rather similar reduction must also be visible in the male organs. So long as these important links are missing there is at least some strong negative evidence against the megaphyllous theory.†




* If it is held, with SOLMS-LAUBACH, that the structure here called a stamen is a male flower (see SCOTT, 1909, p. 537), the above comparison would be still less valid.

† Since the above was written Dr. SCOTT (SCOTT, 1920) has read a paper bearing on the ultimate origin of the Pteridosperms, and expressed the view that they "have always been distinct from any of the known phyla of vascular Cryptogams . . . parallel in important respects to the ferns, but of unknown and remote origin." Unfortunately, my knowledge of this paper is still limited to the brief reference in 'Nature.'

Much has recently been accomplished in connecting up the Cordaiteæ with certain Pteridosperms by means of Cordaitean forms showing an intermediate stem-anatomy, but light has still to be thrown upon the nature of the fructifications borne by these plants. The most recent work on the subject (Scott, 1919) makes it quite probable that one of these Cordaitean stems (*Mesoxylon multirame*) bore the seeds previously described by Mrs. Arber (1910) as *Mitrospermum compressum*, but there is no indication that these seeds make a closer approach, either in their structure or in their mode of attachment, to those of the Pteridosperms, than do those of the other Cordaiteæ.

## Summary.

A description is given of the anatomy of *Acmopyle Pancheri*, Pilger, based chiefly on material from New Caledonia, the native habitat of the plant. Reasons are given for the view that the genus also occurs in the Fiji Islands.

So far as characters of generic rank are concerned, *Acmopyle* does not differ from *Podocarpus* in any of the following features: vegetative anatomy of root, stem and leaf; drupaceous character of the seed, megaspore membrane, female prothallus and young embryo, structure of male cone, microsporophyll, pollen-grain and probably male gametophyte. As is generally the case in *Podocarpus*, the seed is borne on a thick fleshy receptacle composed of the swollen axis and bracts.

The surface of the receptacle is tuberculate, and is raised into more or less prominent humps in the axils of the sterile bracts. The vascular supply to these axillary humps is in the form of paired strands inversely orientated with respect to the subtending bract-traces; the humps are therefore concluded to be vestigial axillary shoots, the entire receptacle being regarded as a reduced branch system. The vascular supply to the ovuliferous organ in the axil of the fertile bract does not differ, except in its much greater degree of development, from that to the humps in the axils of the sterile bracts; the ovuliferous organ is hence regarded as a brachyblast, and homologised with the ovuliferous scale of other Conifers.

*Acmopyle* differs from *Podocarpus*:

(1) In the nearly erect posture of the adult seed;

(2) In the complete fusion of the epimatium to the integument, even in the region of the micropyle, in the formation of which the epimatium takes part;

(3) In the much greater development of the vascular system of the seed, which forms a nearly continuous cup-like tracheal investment covering the basal two-thirds of the stone.

Taking into consideration the entire structure of *Acmopyle*, the genus is concluded to be the most highly specialised of the Podocarpineæ; there appears to be no support for the view that the family is a reduction series with *Podocarpus* as one of its most primitive genera.

The theoretical part of the paper also deals with other controversial questions, namely, the systematic position of the Taxineæ, the morphology of the ovuliferous

scale of Conifers, and the origin of the Conifers. With regard to the first of these questions, the conclusion arrived at is that the structure of the genera *Taxus*, *Torreya*, and *Cephalotaxus* is sufficiently distinct to justify their being placed in a separate phylum, for which the name Taxales is proposed, and which would be equivalent in rank and related to the Ginkgoales and Coniferales. The relations of the Taxales are, it is believed, closer with *Ginkgo* and the Cordaitales than with the Conifers, as here defined.

Concerning the ovuliferous scale of Conifers, the conclusion is in favour of the brachyblast theory.

No definite conclusion is expressed on the question as to whether the Conifers ultimately arose from microphyllous or megaphyllous (fern-like) ancestors, for, although the author confidently believes that they arose from Cordaitalean ancestors, the origin of the Cordaitales themselves from a megaphyllous (fern-like) stock is still considered to be "not proven" on the existing evidence.

Emphasis has been laid upon certain facts of a negative character, which are—pending further evidence—regarded as obstacles in the way of an unqualified acceptance of the megaphyllous theory. Of these facts, special importance is attached to a sharp differentiation that exists between those Gymnosperms (Cycadales, Pteridosperms) in which the seed is clearly borne upon a leaf, and those (Cordaitales, Ginkgoales, Taxales, Coniferales) in which it is either clearly borne directly upon an axis (Cordaitales, *Taxus*), or upon an organ which is probably some modification of an axis (Conifers, *Ginkgo*, etc.). For these two divisions of Gymnosperms, the author proposes the names Phyllosperms (with leaf-borne seeds) and Stachyosperms (with stem-borne seeds) respectively. It is argued that the Cordaitales, being Stachyosperms, cannot have arisen from Phyllosperm ancestors, unless there existed forms which bridge up this and other apparently wide gaps between the two divisions; and of the existence of these intermediate forms there is at present no evidence.

At the same time, it is fully recognised that the meagre evidence of a positive nature that is available at present, is distinctly in favour of a common megaphyllous origin for the Cordaitales and Pteridosperms.

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## EXPLANATION OF PLATES.

### PLATE 9. *Acmopyle Pancheri.*

Fig. 1.—Photograph showing habit. About $\frac{1}{6}$ nat. size.

Fig. 2.—Longitudinal section of young root-tubercle growing out into normal rootlet. Shaded cells in cortex forming an ill-defined infected zone. About × 17.

Fig. 3.—Transverse section of young diarch root. Hoop-like thickenings on inner cortical cells, in section appearing like beads. About × 45.

Fig. 4.—Transverse section of leaf. Compare text-fig. 2, A. *x.*, xylem; *p.*, phloem; *c.*, mucilage canal. About × 28.

Fig. 5.—Section of leaf cut parallel to dorsal surface, showing mosaic of large thin-walled mucilage cells and small crowded palisade cells. About × 100.

Fig. 6.—Section of leaf cut along plane of expansion, showing accessory transfusion tissue. The vascular bundle of the leaf lies not far from the lower edge of the photograph. The upper edge of the photograph shows the leaf margin. About × 25.

Fig. 7.—Camera-lucida drawings of stomata. About × 375.

*a.* Section of leaf cut very nearly parallel to stomatal surface. The stoma towards the lower end of the series was cut very near the cuticle, and shows the deep-staining dorsal lignified lamellæ, and the thickenings of the septa between the guard-cells. The stoma at the upper end was sectioned along a plane midway between the dorsal and ventral lamellæ. The sinuous lines over the septal thickenings are cellulose layers. The walls of the epidermal cells show moniliform thickenings; the cell-contents have been omitted. There is usually one polar subsidiary cell common to two consecutive stomata, and 2–4 lateral subsidiary cells to

each stoma. The lateral subsidiary cells of each stoma touch those of the stomata in front and behind.

*b*. Transverse section through middle of stoma, showing dorsal and ventral lignified lamellæ.

*c*. As we proceed towards the end of a stoma (fig. 7, *c*), the ventral lamellæ gradually vanish, their place being taken by the median septal thickenings; the dorsal lamellæ here stand almost perpendicularly instead of almost horizontally as in the middle region of the stoma.

*d*. Nearly median longitudinal section of stoma. Of the lignified portions only the septal thickenings are seen, besides the lining of the stomatal pore.

Fig. 8.—Median longitudinal section of microstrobilus. ×, organic apex of axis; ✱, peltate terminal stamen, the sterile "shield" forming a (?) protective cap. About × 17.

Fig. 9.—Transverse section of male cone axis, with well-defined epidermal layer of "resin"-cells, and ring of mucilage canals round a circle of strands. The light patches in the canals are coagulated masses of mucilage, one of which contains a deep-stained tabular hexagonal crystal. About × 40.

## Plate 10. *A. Pancheri*.

Fig. 10.—Transverse section of stamen. × ×, points of dehiscence; the figure 10 points to the mucilage canal of the sporophyll strand; the strand itself is not preserved in this section. On the abaxial (lower) side there is a ⅄-shaped air space between the sporangia. About × 32.

Fig. 11.—The same, further enlarged to show reticulate markings on the wings of the pollen-grains, and the thin septum between the sporangia. About × 175.

Fig. 12.—Male inflorescences. Natural size.

Fig. 13.—Transverse section of outer cortex of a receptacle, showing the thick cuticle covering the rounded tubercles; the large clear mucilage cells, and smaller "resin"-cells. About × 35.

Fig. 14.—Part of transverse section of a receptacle, showing the trace of a sterile bract (to the right of the black cross), and two smaller inverted strands (left of the cross) destined to supply an axillary hump. About × 35.

Fig. 15.—Ventral view of stone. The large white spot near the lower end is the eccentric chalaza. The ventral loop of the "escarpment" is not far from the chalaza. About × 3.

Fig. 16.—Dorsal view of stone. The chalaza is invisible from this side, and the dorsal loop of the "escarpment" is nearer the micropyle than it is in fig. 15. About × 3.

Fig. 17.—Basal view of stone, showing the eccentric chalaza and the radiating marks corresponding to the strands in the flesh. About × 3.

Fig. 18.—View of stone from the left side. One arrow points towards the chalaza, the other away from the micropyle. A curved faintly prominent ridge connects the two points. Note the relative positions of the two loops of the "escarpment" with respect to the chalaza. About × 3.

Fig. 19.—Apical view of stone. The micropyle is just visible as a minute black spot in the centre. About × 3.

PLATE 11. *A. Pancheri.*

Fig. 20.—Part of transverse section of seed, at about the level of text-fig. 32 (compare index-figure on p. 275). *o.o.f.*, outer zone of outer flesh; *i.o.f.*, inner zone of outer flesh; *scl.*, sclerotesta; *cup.*, vascular cupule; just inside this point a strand is seen coming off from the inner face of the cupule.

The horizontal line indicates the plane of dehiscence of the stone. Note that the ventral (upper) valve is considerably larger than the dorsal. The arrow points to one of the carinæ of the sclerotesta. About × 5½.

Fig. 21.—Transverse section of seed, cut at about the level of text-fig. 32 (see also text-fig. 35). The vascular cupule is seen in section as a faint white line with moniliform thickenings. Slightly larger than natural size.

Fig. 22.—Megastrobilus. *a.* Oblique dorsal view of two strobili on a forked, strongly curved peduncle. The curved ridge on the back of the seed, the tuberculate surface of the receptacle with the sterile bracts, and the broad fertile bract wedged in between the receptacle and seed, are clearly seen. Nat. size.

*b.* Ventral view of a strobilus attached to a pectinate shoot. In the natural position of the organs, if the shoot is seen from the upper side (as in our photograph) the fruit would be concealed beneath it. In order to expose it to the view, the fruit has been moved out of its natural position. The sub-apical micropyle is well seen, but the curved ridge is invisible from this side. Nat. size.

*c.* Median longitudinal section of fruit. Nat. size.

Fig. 23.—Ventral view of a megastrobilus, showing (1) the large round hump on the receptacle, with the most distal sterile bract projecting from its centre (just below the seed); and (2) three other sterile bracts (two right and left and one in the middle below), each with an axillary hump. Nat. size.

Fig. 24.—View from left side of a seed from which the outer zone of the outer flesh was shaved off so as to expose the vascular cupule, stiffened by a network of strands. The two basal strands are also exposed. Comparison with Plate 2, fig. 18, shows that the cupule does not extend beyond the "escarpment."

The seed was photographed while immersed in alcohol, for then the xylem appeared white and showed up well against the "resinous" inner zone of the flesh. Slightly larger than natural size.

Fig. 25.—The dome-shaped free portion of a nucellus, flattened out under a coverslip after removal of the nucellar cone, of which the scar is indicated by an arrow. Round this scar is a broad areole of light colour, which contrasts well with the dark peripheral part rich in "resin"-cells. About × 20.

Fig. 26.—Apical part of megaspore, with a pro-embryo to one side of the axis. The coiled suspensor tubes are seen cut in different planes. The apex of the megaspore is produced into a blunt process which may (?) be likened to the "tent-pole" of *Ginkgo*. About × 11.

Fig. 27.—Drawings to show the different types of tracheides in the vascular cupule of the seed.

Fig. 28.—Superficial cells of megaspore, with poorly developed megaspore membrane, and anticlinal walls specially thickened next to the membrane.

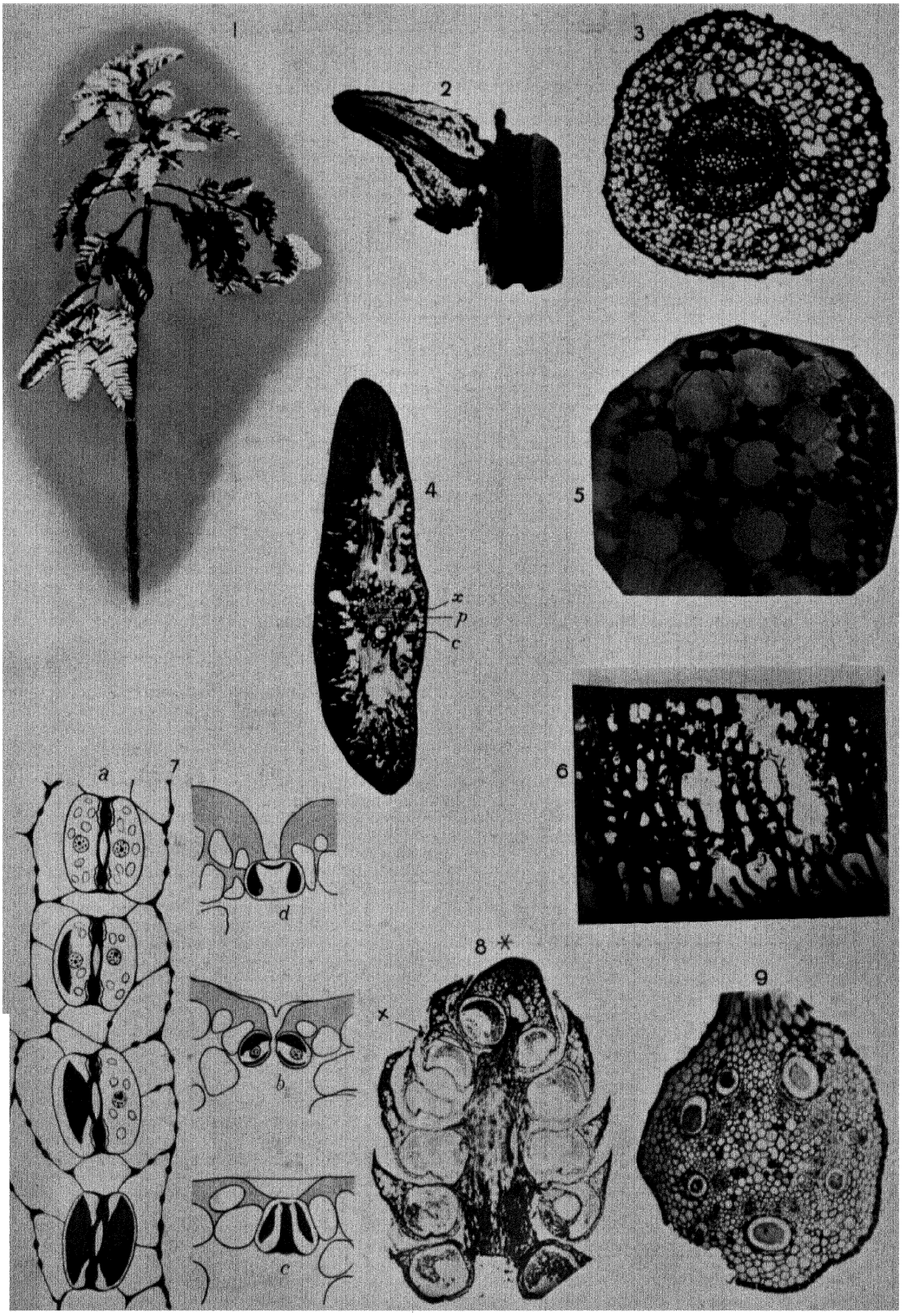
Fig. 29.—Surface view of superficial layer of megaspore. The multinucleate cells have their thickened anticlinal walls perforated by straight pits which impart a prismatic appearance to the walls.

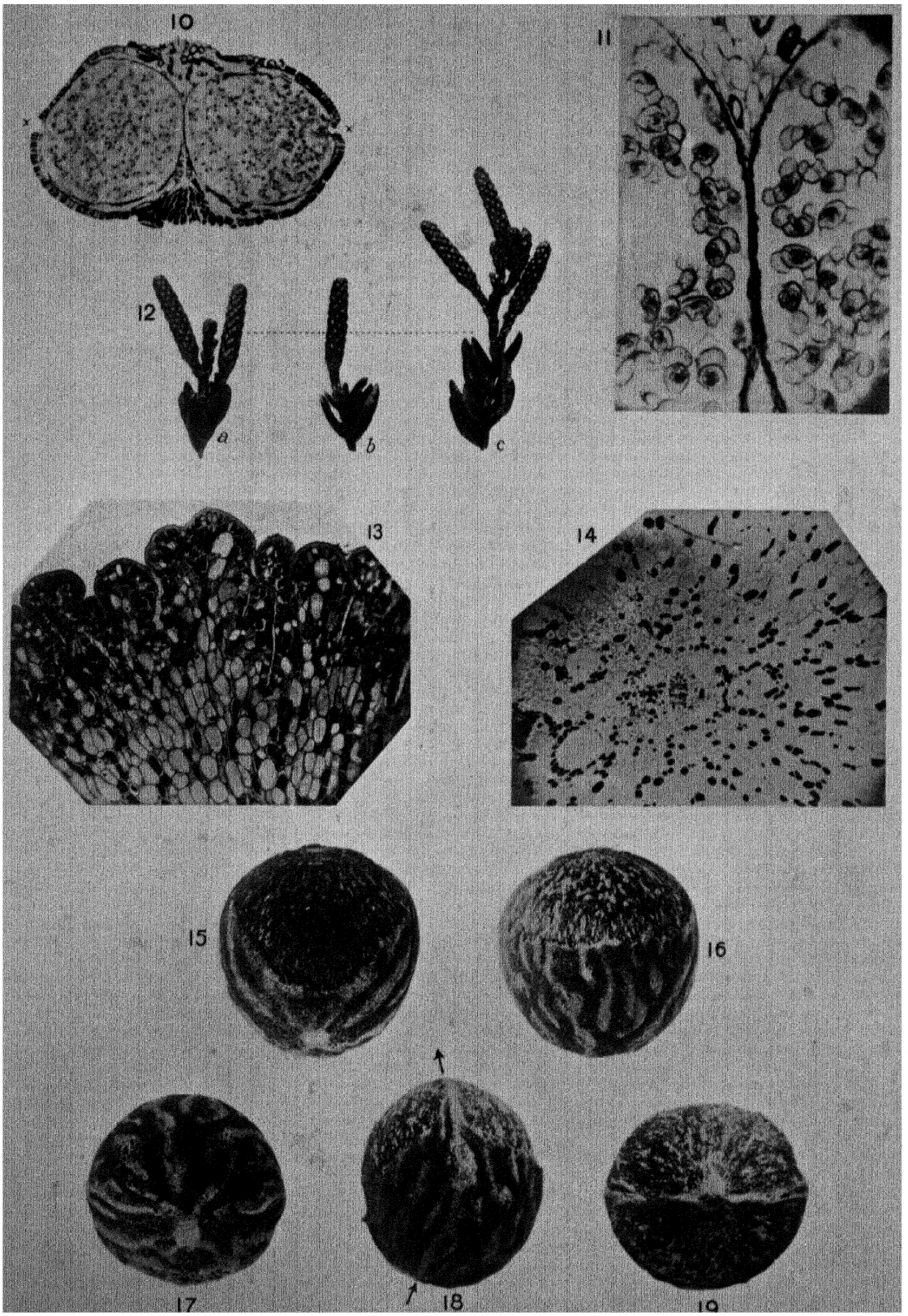
*Podocarpus imbricatus.*

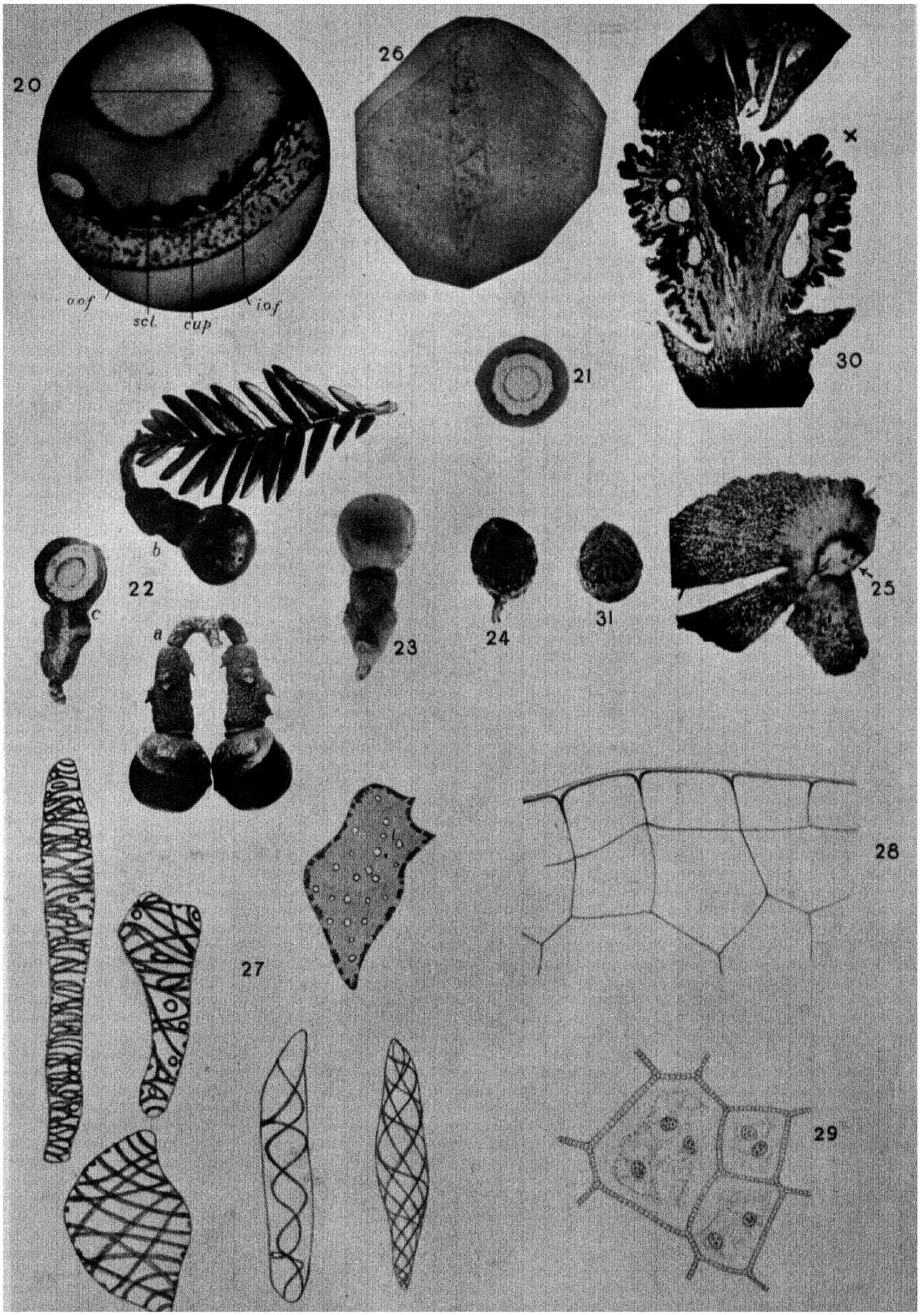
Fig. 30.—Longitudinal section of receptacle and micropylar region of seed. As in *Acmopyle* the receptacle has a tuberculate surface (compare Plate 11, figs. 22*a*, 23). At × there was a sterile bract (in a position corresponding to that of the last sterile bract of *Acmopyle*, see Plate 11, fig. 23), but this was removed before the section was prepared. About × 17.

*Podocarpus sp.*

Fig. 31.—Stone of a new species discovered by COMPTON in New Caledonia. The sculpturing shows a general similarity to that in *Acmopyle* (see Plate 10, fig. 15). Slightly enlarged.


1
2
3
4
x
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c
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a
d
b
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9


10
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