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LESSONS

IN

ELEMENTARY BIOLOGY

BY THE LATE

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WITH ONE HUNDRED AND TWENTY-SEVEN ILLUSTRATIONS

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PREFACE TO THE FIRST EDITION

In his preface to the new edition of the well-known *Practical Biology*, Professor Huxley gives his reasons for beginning the study of organised nature with the higher forms of animal life, to the abandonment of his earlier method of working from the simpler to the more complex organisms. He says in effect that experience has taught him the unwisdom of taking the beginner at once into the new and strange region of microscopic life, and the advantage of making him commence his studies with a subject of which he is bound to know something - the elementary anatomy and physiology of a vertebrate animal.

Most teachers will probably agree with the general truth of this opinion. The first few weeks of the beginner in natural science are so fully occupied in mastering an unfamiliar and difficult terminology and in acquiring the art of using his eyes and fingers, that he is simply incapable for a time of grasping any of the principles of the science; and, this being the case, the more completely his new work can

be connected with any knowledge of the subject, however vague, he may already possess, the better for his progress.

On the other hand, the advantage to logical treatment of proceeding from the simple to the complex -of working upwards from protists to the higher plants and animals -is so immense that it is not to be abandoned without very good and sufficient reasons.

In my own experience I have found that the difficulty may be largely met by a compromise, namely, by beginning the work of the class by a comparative study of one of the higher plants (flowering plant or fern) and of one of the higher animals (rabbit, frog, or crayfish). If there were no limitations as to time, and if it were possible to avoid altogether the valley of the shadow of the coming examination, this preliminary work might be extended with advantage, and made to include a fairly complete although elementary study of animal physiology, with a minimum of anatomical detail, and a somewhat extensive study of flowering plants with special reference to their physiology and to their relations to the rest of nature.

In any case by the time this introductory work is over, the student of average intelligence has overcome preliminary difficulties, and is ready to profit by the second and more systematic part of the course in which organisms are studied in the order of increasing complexity.

It is such a course of general elementary biology which I have attempted to give in the following Lessons, my aim having been to provide a book which may supply in the study the place occupied in the laboratory by "Huxley and Martin," by giving the connected narrative which would be

out of place in a practical handbook. I also venture to hope that the work may be of some use to students who have studied zoology and botany as separate subjects, as well as to that large class of workers whose services to English science often receive but scant recognition - I mean amateur microscopists.

As to the general treatment of the subject I have been guided by three principles. Firstly, that the main object of teaching biology as part of a liberal education is to familiarise the student not so much with the facts as with the ideas of science. Secondly, that such ideas are best understood, at least by beginners, when studied in connection with concrete types of animals and plants. And, thirdly, that the types chosen should illustrate without unnecessary complication the particular grade of organisation they are intended to typify, and that exceptional cases are out of place in an elementary course.

The types have therefore been selected with a view of illustrating all the more important modifications of structure and the chief physiological processes in plants and animals; and, by the occasional introduction of special lessons on such subjects as biogenesis, evolution, &c., the entire work is so arranged as to give a fairly connected account of the general principles of biology. It is in obedience to the last of the principles just enunciated that I have described so many of the Protozoa, omitted all but a brief reference to the development of Hydra and to the so-called sexual process in Penicillium, and described Nitella, instead of Chara, and Polygordius instead of the earthworm. The last-named substitution is of course only made possible by the book

being intended for the study and not for the laboratory, but I feel convinced that the student who masters the structure of Polygordius, even from figures and descriptions alone, will be in a far better position to profit by a practical study of one of the higher worms.

Lessons XXVII. and XXX.[1] are mere summaries, and can only be read profitably by those who have studied the organisms described, or allied forms, in some detail. Such abstracts were however necessary to the plan of the book, in order to show how all the higher animals and plants may be described, so to speak, in terms of Polygordius and of the fern.

For many years I have been convinced of the urgent need for a unification of terminology in biology, and have now attempted to carry out a consistent scheme, as will be seen by referring to the definitions in the glossary. Many of Mr. Harvey Gibson's suggestions are adopted, and three new words are introduced—phyllula, gamobium, and agamobium. I expect and perhaps deserve to be criticised, or, what is worse, let alone, for the somewhat extreme step of using the word *ovary* in its zoological sense throughout the vegetable kingdom ; and for describing as the *venter* of the pistil the so-called ovary of Angiosperms. I would only beg my critics before finally pronouncing judgment to try and look at the book, from the point of view of the beginner, as a graduated course of instruction, and to consider the effect upon the entire scheme of using a term of fundamental importance in two utterly different senses.

A large proportion of the figures are copied either from

[1] See Preface to the Third Edition, p. xi.

original sources or from my own drawings—the latter when no authority is mentioned. The majority, even of those which have previously appeared in text-books, have been specially engraved for the work, the draughtsman being my brother, Mr. M. P. Parker. In order to facilitate reference the illustrations referring to each subject have, as far as possible, been grouped together, so that the actual is considerably larger than the nominal number of figures. Full descriptions are given instead of mere lists of reference-letters: these will, I hope, be found useful as abstracts of the subjects illustrated.

I have to thank my friends Mr. A. Dillon Bell and Professor J. H. Scott, M.D., for constant and valuable help in criticising the manuscript. To Dr. Paul Meyer, of the Zoological Station, Naples, I am indebted for specimens of Polygordius; and to Professor Sale, of this University, Professor Haswell, of Sydney, Professor Thomas, of Auckland, and Professors Howes and D. H. Scott, of South Kensington, for important information and criticism on special points. My brother, Professor W. Newton Parker, has kindly promised to undertake a final revision for the press.

DUNEDIN, N.Z.,
August 1890.

PREFACE TO THE THIRD EDITION

In the two former editions the "Lessons" practically concluded with Polygordius as an example of tripoblastic animals, and with the Fern as an example of vascular plants, and the merest sketches of the higher groups of both kingdoms were added (see Preface to the first edition, p. viii). It has, however, been suggested to me from more than one source, that the usefulness of the book would be increased by expanding these sketches into something more comprehensible to the beginner.

This I have done in the present edition, with the result that Lesson XXVII. of previous editions has been expanded into Lessons XXVI.—XXIX., and Lesson XXX. into Lessons XXXII.—XXXIV. The new matter is illustrated with forty additional figures.

I have again to thank my brother, Prof. W. N. Parker, for sacrificing much time in the labour of proof correcting.

September 1896.

TABLE OF CONTENTS

PAGE

PREFACE TO THE FIRST EDITION v

PREFACE TO THE THIRD EDITION xi

LIST OF ILLUSTRATIONS xix

LESSON I.

AMŒBA 1

LESSON II.

HÆMATOCOCCUS 23

LESSON III.

HETEROMITA 36

LESSON IV.

EUGLENA 44

LESSON V.

PROTOMYXA AND THE MYCETOZOA 49

LESSON VI.

PAGE

A COMPARISON OF THE FOREGOING ORGANISMS WITH CERTAIN CONSTITUENT PARTS OF THE HIGHER ANIMALS AND PLANTS 56

ANIMAL AND PLANT CELLS 56

MINUTE STRUCTURE AND DIVISION OF CELLS AND NUCLEI 62

OVA OF ANIMALS AND PLANTS 69

LESSON VII.

SACCHAROMYCES 71

LESSON VIII.

BACTERIA 82

LESSON IX.

BIOGENESIS AND ABIOGENESIS 95

HOMOGENESIS AND HETEROGENESIS 102

LESSON X.

PARAMŒCIUM 106

STYLONYCHIA 116

OXYTRICHA 120

LESSON XI.

OPALINA 121

LESSON XII.

VORTICELLA 126

ZOOTHAMNIUM 135

LESSON XIII.

PAGE
SPECIES AND THEIR ORIGIN: THE PRINCIPLES OF CLASSIFICATION 137

LESSON XIV.

THE FORAMINIFERA 148
THE RADIOLARIA 152
THE DIATOMACEÆ 155

LESSON XV.

MUCOR 158

LESSON XVI.

VAUCHERIA 169
CAULERPA . . 175

LESSON XVII.

THE DISTINCTIVE CHARACTERS OF ANIMALS AND PLANTS . . 176

LESSON XVIII.

PENICILLIUM 184
AGARICUS 191

LESSON XIX.

SPIROGYRA 194

LESSON XX.

MONOSTROMA 201
ULVA 203
NITELLA 203

LESSON XXI.

PAGE

HYDRA 218

LESSON XXII.

HYDROID POLYPES 234

BOUGAINVILLEA, &c. 234

DIPHYES 248

PORPITA 249

LESSON XXIII.

SPERMATOGENESIS AND OOGENESIS 253

THE MATURATION AND IMPREGNATION OF THE OVUM 258

THE CONNECTION BETWEEN UNICELLULAR AND DIPLOBLASTIC ANIMALS 261

LESSON XXIV.

POLYGORDIUS 268

LESSON XXV.

POLYGORDIUS (*continued*) 290

LESSON XXVI.

THE CHIEF DIVISIONS OF THE ANIMAL KINGDOM 304

THE STARFISH 306

LESSON XXVII.

THE CRAYFISH 318

LESSON XXVIII.

THE FRESH-WATER MUSSEL 348

LESSON XXIX.

PAGE
THE DOGFISH 366

LESSON XXX.

MOSSES 400

LESSON XXXI.

FERNS 412

LESSON XXXII.

THE CHIEF DIVISIONS OF THE VEGETABLE KINGDOM . . 431
EQUISETUM 434
SALVINIA 438
SELAGINELLA 442

LESSON XXXIII.

GYMNOSPERMS 447

LESSON XXXIV.

ANGIOSPERMS 461

SYNOPSIS 477

INDEX AND GLOSSARY 487

LIST OF ILLUSTRATIONS

FIG.		PAGE
1.	*Amœba*, various species	2
2.	*Protamœba primitiva*	9
3.	*Hæmatococcus pluvialis* and *H. lacustris*	24
4.	*Heteromita rostrata*	38
5.	*Euglena viridis*	45
6.	*Protomoyxa aurantiaca*	50
7.	*Badhamia* and *Physarum*	53
8.	Typical animal and vegetable cells	57
9.	Animal and plant cells, detailed structure	62
10.	Diagram illustrating the process of indirect cell-division	64
11.	Ova of *Carmarina* and *Gymnadenia*	69
12.	*Saccharomyces cerevisiæ*	72
13.	*Bacterium termo*	83
14.	*Bacterium termo*, showing flagella	84
15.	*Micrococcus*	86
16.	*Bacillus subtilis*	87
17.	*Vibrio serpens*, *Spirillum tenue*, and *S. volutans*	88
18.	*Bacillus anthracis*	90
19.	Beaker with culture-tubes	100
20.	*Paramœcium caudatum*	108
21.	*Paramœcium caudatum*, conjugation	115
22.	*Stylonychia mytilus*	117

FIG.		PAGE
23.	*Oxytricha flava*	120
24.	*Opalina ranarum*	122
25.	*Vorticella*	127
26.	*Zoothamnium arbuscula*	134
27.	*Zoothamnium*, various species	138
28.	Diagram illustrating the Origin of the Species of *Zoothamnium* by Creation	142
29.	Diagram illustrating the Origin of the Species of *Zoothamnium* by Evolution	144
30.	*Rotalia*	149
31.	Diagrams of *Foraminifera*	150
32.	*Alveolina quoii*	151
33.	*Lithocircus annularis*	152
34.	*Actinomma asteracanthion*	153
35.	Diagrams of a Diatom and shells of *Navicula* and *Aulacodiscus*	156
36.	*Mucor mucedo* and *M. stolonifer*	159
37.	Moist Chamber	163
38.	*Vaucheria*	170
39.	*Caulerpa scalpelliformis*	175
40.	*Penicillium glaucum*	186
41.	*Agaricus campestris*	192
42.	*Spirogyra*	195
43.	*Monostroma bullosum* and *M. laceratum*	202
44.	*Nitella*, general structure	204
45.	*Nitella*, terminal bud	209
46.	*Nitella*, spermary	212
47.	*Nitella*, ovary	214
48.	*Chara*, pro-embryo	216
49.	*Hydra viridis* and *H. fusca*, external form	219
50.	*Hydra*, minute structure	223
51.	*Hydra*, nematocyst and nerve-cell	225
52.	*Hydra viridis*, ovum	232
53.	*Bougainvillea ramosa*	235
54.	*Eucopella*, portion of tentacle	237

FIG.		PAGE
55.	Diagrams illustrating derivation of *Medusa* and *Hydranth*	241
56.	*Eucopelia campanularia*, muscle fibres and cells	243
57.	*Laomedea flexuosa* and *Eudendrium ramosum*, development.	247
58.	*Diphyes campanulata*	250
59.	*Porpita pacifica* and *P. mediterranea*	251
60.	Spermatogenesis in the Mole-cricket	254
61.	Ovum of *Toxopneustes lividus*	257
62.	Maturation and impregnation of the animal ovum	258
63.	*Pandorina morum*	263
64.	*Volvox globator*	265
65.	*Volvox globator*	266
66.	*Polygordius neapolitanus*, external form	269
67.	*Polygordius neapolitanus*, anatomy	271
68.	*Polygordius neapolitanus*, nephridium	282
69.	*Polygordius*, diagram illustrating the relations of the nervous-system	284
70.	*Polygordius neapolitanus*, reproductive organs	291
71.	*Polygordius neapolitanus*, larva in the trochosphere stage	293
72.	Diagram illustrating the origin of the trochosphere from the gastrula	295
73.	*Polygordius neapolitanus*, advanced trochosphere	297
74.	*Polygordius neapolitanus*, larva in a stage intermediate between the trochosphere and the adult	300
75.	Starfish, ventral aspect	307
76.	Starfish, diagrammatic sections	309
77.	Starfish, digestive organs	311
78.	Starfish, water vascular system	313
79.	Starfish, early stages in development	316
80.	Starfish, development of bipinnaria larva	317
81.	Crayfish, side view	319
82.	Crayfish, principal appendages	322
83.	Crayfish, diagrammatic sections	328
84.	Crayfish, action of abdominal muscles	330
85.	Crayfish, leg, with muscles	331
86.	Crayfish, dissection	333

FIG.		PAGE
87.	Crayfish, gills	336
88.	Crayfish, diagram of circulation of blood	340
89.	Crayfish, early development	344
90.	Crayfish, early embryo in nauplius stage	345
91.	Crayfish, later embryo	346
92.	Mussel, side view, and shell	351
93.	Mussel, diagrammatic sections	353
94.	Mussel, dissection	356
95.	Mussel, structure of gill	358
96.	Mussel, circulatory system	361
97.	Mussel, advanced embryo and free larva	364
98.	Dogfish, side view	367
99.	Dogfish, diagrammatic sections	370
100	Dogfish, skull	373
101.	Dogfish, vertebræ	376
102.	Dogfish, pectoral arch	378
103.	Dogfish, dissection	380
104.	Dogfish, vascular system	385
104a.	Dogfish, diagram of circulation	389
105.	Dogfish, brain	392
106.	Dogfish, early embryo	398
107.	Dogfish, advanced embryo	399
108.	Mosses, various genera, anatomy and histology	402
109.	*Funaria*, reproduction and development	406
110.	*Pteris* and *Aspidium*, anatomy and histology	414
111.	Ferns, various genera, reproduction and development	424
112.	*Equisetum*, aërial shoot and spores	435
113.	*Equisetum*, reproduction and development	437
114.	*Salvinia*, part of plant	439
115.	*Salvinia*, reproduction and development	441
116.	*Selaginella*, part of plant and sporangia	443
117.	*Selaginella*, reproduction and development	445
118.	*Pinus*, sections of stem	449
119.	Gymnosperms, reproduction and development	453
120.	*Pinus*, stamen	455

FIG. PAGE
121. *Pinus*, carpel 456
122. *Zamia* and *Cycas*, reproductive organs 457
123. Lily, section of stem 462
124. Buttercup, structure of flower 465
125. Transition from petal to stamen 467
126. Angiosperms, reproduction and development 470
127. *Helleborus*, *Campanula*, and *Ribes*, flower 472

LESSONS

IN

ELEMENTARY BIOLOGY

LESSON I

'AMŒBA

It is hardly possible to make a better beginning of the systematic study of Biology than by a detailed examination of a microscopic animalcule often found adhering to weeds and other submerged objects in stagnant water, and known to naturalists as *Amœba*.

Amœbæ are mostly invisible to the naked eye, rarely exceeding one-fourth of a millimetre ($\frac{1}{100}$ inch) in diameter, so that it is necessary to examine them entirely by the aid of the microscope. They can be seen and recognised under the low power of an ordinary student's microscope which magnifies from twenty-five to fifty diameters; but for accurate examination it is necessary to employ a far higher power, one in fact which magnifies about 300 diameters.

Seen under this power, an Amœba appears like a little

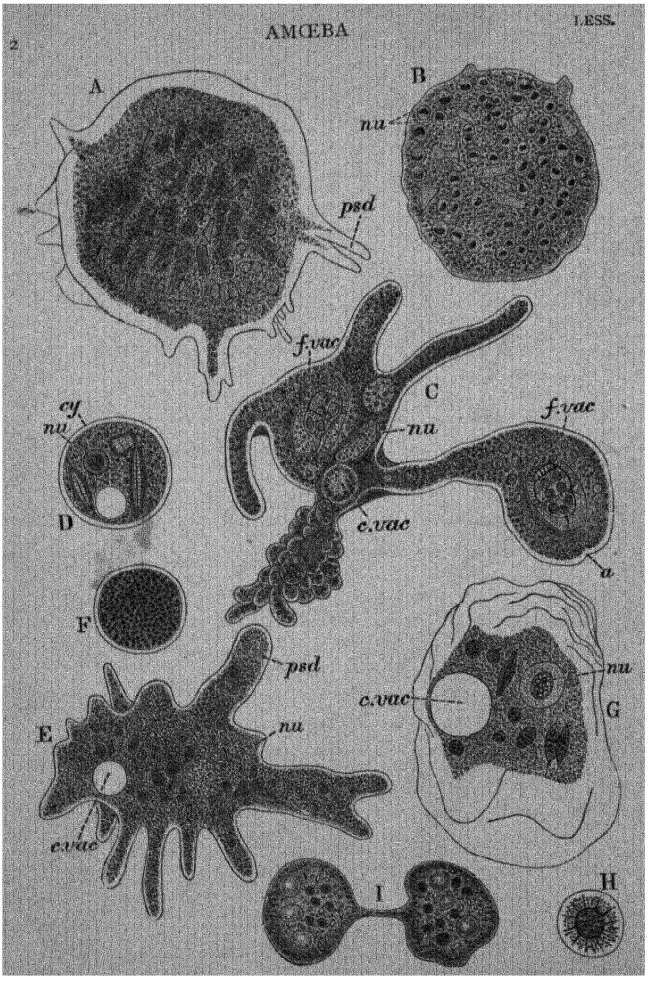

FIG. 1. *Amœba guarna*, a living specimen, showing granular endosarc surrounded by clear ectosarc, and several pseudopods

some formed of ectosarc only, others containing a core of endosarc. The larger bodies in the endosarc are mostly food-particles (× 300).[1]

B. The same species, killed and stained with carmine to show the numerous nuclei (*nu*) (× 300).

C. *Amœba proteus*, a living specimen, showing large irregular pseudopods, nucleus (*nu*), contractile vacuole (*c. vac*), and two food vacuoles (*f. vac*), each containing a small infusor (see Lesson X.) which has been ingested as food. The letter *a* to the right of the figure indicates the place where the protoplasm has united round the prey to inclose the food vacuole. The contractile vacuole in this figure is supposed to be seen through a layer of granular protoplasm, whereas in the succeeding figures (D, E, and G) it is seen in optical section, and therefore appears clear.

D. An encysted Amœba, showing cell-wall or cyst (*cy*), nucleus (*nu*), clear contractile vacuole, and three diatoms (see Lesson XIV.) ingested as food.

E. *Amœba proteus*, a living specimen, showing several large pseudopods (*psd*), single nucleus (*nu*), and contractile vacuole (*c. vac*), and numerous food-particles embedded in the granular endosarc (× 330).

F. Nucleus of the same after staining, showing a ground substance of nuclear sap, containing deeply-stained granules of chromatin, and surrounded by a distinct membrane (× 1010).

G. *Amœba verrucosa*, living specimen, showing wrinkled surface, nucleus (*nu*), large contractile vacuole (*c. vac*), and several ingested organisms (× 330).

H. Nucleus of the same, stained, showing the chromatin aggregated in the centre (× 1010).

I. *Amœba proteus*, in the act of multiplying by binary fission (× 500).

(A, B, E, F, G, and H after Gruber; C and I after Leidy; D after Howes.)

shapeless blob of jelly, nearly or quite colourless. The central part of it (Fig. I, A, C, and E) is granular and semi-transparent—something like ground glass—while surrounding this inner mass is a border of perfectly transparent and colourless substance. So clear, indeed, is this outer layer that it is easily overlooked by the beginner, who is apt to take the granular internal substance for the whole Amœba. If in any way the creature can be made to turn over, or if a number of specimens are examined in various positions, these two constituents will always be found to have the

[1] A number preceded by the sign of multiplication indicates the number of diameters to which the object is magnified.

same relations, whence we conclude that an Amœba consists of a granular substance the *endosarc*, completely surrounded by a clear transparent layer or *ectosarc*.

One very noticeable thing about Amœba is that it is never of quite the same shape for long together. Often the changes of form are so slow as to be almost imperceptible, like the movements of the hour-hand of a watch, but by examining it at successive intervals the alteration becomes perfectly obvious, and at the end of half an hour it will probably have altered so much as to be hardly like the same thing.

In an active specimen the way in which the changes of form are brought about is easily seen. At a particular point the ectosarc is pushed out in the form of a small pimple-like elevation (Fig. I, A, left side): this increases in size, still consisting of ectosarc only, until at last granules from the endosarc stream into it, and the projection or *pseudopod* (A, C, E, *psd*) comes to have the same structure as the rest of the Amœba. It must not be forgotten that the animal does not alter perceptibly in volume during the process, every pseudopod thus protruded from one part of the body necessitating the withdrawal of an equal volume for some other part.

This peculiar mode of movement may be illustrated by taking an irregular lump of clay or putty and squeezing it between the fingers. As it is compressed in one direction it will elongate in another, and the squeezing process may be regulated so as to cause the protrusion of comparatively narrow portions from the solid lump, when the resemblance to the movements described in the preceding paragraph will be fairly close. Only it must be borne in mind that in Amœba there is no external compression, the "squeezing" being done by the animalcule itself.

The occurrence of these movements is alone sufficient to show that Amœba is an *organism* or living thing, and no mere mass of dead matter.

The jelly-like substance of which Amœba is composed is called *protoplasm.* It is shown by chemical analysis[1] to consist mainly of certain substances known as *proteids*, bodies of extreme complexity in chemical constitution, the most familiar example of which is white of egg or albumen. They are compounds of carbon, hydrogen, oxygen, nitrogen, and sulphur, the five elements being combined in the following proportions :—

Carbon .	. from	51·5	to	54·5	*per cent.*
Hydrogen .	„	6·9	„	7·3	„ „
Oxygen .	„	20·9	„	23·5	„ „
Nitrogen .	„	15·2	„	17·0	„ „
Sulphur .	„	0·3	„	2·0	„ „

Besides proteids, protoplasm contains small proportions of mineral matters, especially phosphates and sulphates of potassium, calcium, and magnesium. It also contains a considerable quantity of water which, being as essential a constituent of it as the proteids and the mineral salts, is called *water of organization.*

Protoplasm is dissolved by prolonged treatment with weak acids or alkalies. Strong alcohol coagulates it, *i.e.*, causes it to shrink by withdrawal of water and become comparatively hard and opaque. Coagulation is also produced by raising the temperature to about 40° C.; the reader will remember how the familiar proteid white of egg is coagulated and rendered hard and opaque by heat.

[1] Accurate analyses of the protoplasm of Amœba have not been made, but the various micro-chemical tests which can be applied to it leave no doubt that it agrees in all essential respects with the protoplasm of other organisms, the composition of which is known (see p. 7).

There is another important property of proteids which is tested by the instrument called a dialyser. This consists essentially of a shallow vessel, the bottom of which is made of bladder, or vegetable parchment, or some other organic (animal or vegetable) membrane. If a solution of sugar or of salt is placed in a dialyser and the instrument floated in a larger vessel of distilled water, it will be found after a time that some of the sugar or salt has passed from the dialyser into the outer vessel through the membrane. On the other hand, if a solution of white of egg is placed in the dialyser no such transference to the outer vessel will take place.

The dialyser thus allows us to divide substances into two classes: *crystalloids*—so called because most of them, like salt and sugar, are capable of existing in the form of crystals—which, in the state of solution, will diffuse through an organic membrane; and *colloids* or glue-like substances which will not diffuse. Protoplasm, like the proteids of which it is largely composed, is a colloid, that is, is non-diffusible. It has a slightly alkaline reaction.

Another character of proteids is their *instability*. A lump of salt or of sugar, a piece of wood or of chalk, may be preserved unaltered for any length of time, but a proteid if left to itself very soon begins to *decompose;* it acquires an offensive odour, and breaks up into simpler and simpler compounds, the most important of which are water (H_2O), carbon dioxide or carbonic acid (CO_2), ammonia (NH_3), and sulphuretted hydrogen (H_2S).[1] In this character of instability or readiness to decompose protoplasm notoriously agrees with its constituent proteids; any dead organism will,

[1] For a more detailed account of the phenomena of putrefaction see Lesson VIII., in which it will be seen that the above statement as to the instability of (dead) proteids requires qualification; as a matter of fact they decompose only in the presence of living Bacteria.

unless special means are taken to preserve it, undergo more or less speedy decomposition.

Many of these properties of protoplasm can hardly be verified in the case of Amœba, owing to its minute size and the difficulty of isolating it from other organisms (water-weeds, &c.) with which it is always associated; but there are some tests which can be readily applied to it while under observation beneath the microscope.

One of the most striking of these micro chemical tests depends upon the avidity with which protoplasm takes up certain colouring matters. If a drop of a neutral or slightly alkaline solution of carmine or logwood, or of some aniline dye, or a weak solution of iodine, is added to the water containing Amœba, the animalcule is killed, and at the same time becomes more or less deeply stained.

The staining is, however, not uniform. The endosarc, owing to the granules it contains, appears darker than the ectosarc, and there is usually to be seen, in the endosarc, a rounded spot more brightly stained than the rest. This structure, which can sometimes be seen in the living Amœba (Fig. I, C, E, and G, *nu*), while frequently its presence is revealed only by staining (comp. A and B), is called the *nucleus*.

But when viewed under a sufficiently high power, the nucleus itself is seen to be unequally stained. It has lately been shown, in many Amœbæ, to be a globular body, enclosed in a very delicate membrane, and made up of two constituents, one of which is deeply stained by colouring matters, and is hence called *chromatin*, while the other, the *nuclear sap* or *achromatin*, takes a lighter tint (Fig. I, F). The relative arrangement of chromatin and sap varies in different Amœbæ: sometimes there are granules of chromatin in an achromatic ground substance (F); some-

times the chromatin is collected towards the surface or periphery of the nucleus; sometimes, again, it becomes aggregated in the centre (G, H). One or more smaller bodies, or *nucleoli*, may also be present in the nucleus, which is then distinguished as the *nucleolus*.

When it is said that Amœbæ sometimes have one kind of nucleus and sometimes another, it must not be inferred that the same animalcule varies in this respect. What is meant is that there are found both in fresh and salt water many kinds or *species* of Amœba which are distinguished from one another, amongst other things, by the character of their nuclei, just as the various species of *Felis*—the cat, lion, tiger, lynx, &c.—are distinguished from one another, amongst other things, by the colour and markings of their fur. According to the method of *binomial nomenclature* introduced into biology by Linnæus, the same *generic name* is applied to all such closely allied species, while each is specially distinguished by a second or *specific name* of its own. Thus under the *genus* Amœba are included *Amœba proteus* (Fig. I, C, E, and F), with long lobed pseudopods and a nucleus containing evenly-disposed granules of chromatin; *A. quarta* (A and B), with short pseudopods and numerous nuclei; *A. verrucosa* (G and H) with crumpled or folded surface, no well-marked pseudopods, and a nucleus with a central aggregation of chromatin substance; and many others.

Besides the nucleus, there is another structure frequently visible in the living Amœba. This is a clear, rounded space in the protoplasm (C, E, and G, *c. vac*), which periodically disappears with a sudden contraction and then slowly reappears, its movements reminding one of the beating of a minute colourless heart. It is called the *contractile vacuole*, and consists of a cavity containing a watery fluid.

Occasionally Amœbæ—or more strictly Amœba like organisms—are met with which show neither nucleus[1] nor contractile vacuole, and are therefore placed in the separate genus *Protamœba* (Fig. 2). They may be looked upon as the simplest of living things.

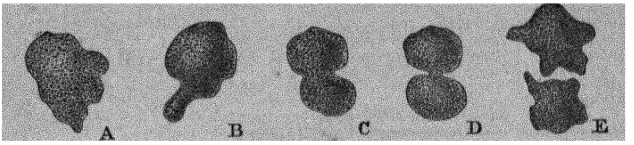

FIG. 2—*Protamœba primitiva*, A, B, the same specimen drawn at short intervals of time, showing changes of form.
C—E. Three stages in the process of binary fission. (After Haeckel.)

The preceding paragraphs may be summed up by saying that Amœba is a mass of protoplasm produced into temporary processes or pseudopods, divisible into ectosarc and endosarc, and containing a nucleus and a contractile vacuole: that the nucleus consists of two substances, chromatin and nuclear sap, enclosed in a distinct membrane: and that the contractile vacuole is a mere cavity in the protoplasm containing fluid. All these facts come under the head of *Morphology*, the division of biology which treats of form and structure: we must now study the *Physiology* of our animalcule—that is, consider the actions or *functions* it is capable of performing.

First of all, as we have already seen, it moves, the movement consisting in the slow protrusion and withdrawal of pseudopods. This may be expressed generally by saying

[1] Judging from the analogy of the Infusoria it seems very probable that such apparently non-nucleate forms as Protamœba contain chromatin diffused in the form of minute granules throughout their substance (see end of Lesson X., p. 120), or that they are forms which have lost their nuclei.

that Amœba is *contractile*, or that it exhibits *contractility*. But here it must be borne in mind that contraction does not mean the same thing in biology as in physics. When it is said that a red-hot bar of iron contracts on cooling, what is meant is that there is an actual reduction in volume, the bar becoming smaller in all dimensions. But when it is said that an Amœba contracts, what is meant is that it diminishes in one dimension while increasing in another, no perceptible alteration in volume taking place: each time a pseudopod is protruded an equivalent volume of protoplasm is withdrawn from some other part of the body.

We may say then that contractility is a function of the protoplasm of Amœba—that is, that it is one of the actions which the protoplasm is capable of performing.

A contraction may arise in one or other of two ways. In most cases the movements of an Amœba take place without any obvious external cause; they are what would be called in the higher animals voluntary movements—movements dictated by the will and not necessarily in response to any external stimulus. Such movements are called *spontaneous* or *automatic*. On the other hand, movements may be induced in Amœba by external stimuli, by a sudden shock, or by coming into contact with an object suitable for food: such movements are the result of *irritability* of the protoplasm, which is thus both automatic and irritable—that is, its contractility may be set in action either by internal or by external stimuli.

Under certain circumstances an Amœba temporarily loses its power of movement, draws in its pseudopods, and becomes a globular mass around which is formed a thick, shell-like coat, called the *cyst* or *cell-wall* (Fig. 1, D, *cy*). The composition of this is not known; it is certainly not

protoplasmic, and very probably consists of some nitrogenous substance allied in composition to horn and to the chitin which forms the external shell of crustacea, insects, &c. After remaining in this *encysted* condition for a time, the Amœba escapes by the rupture of its cell-wall, and resumes active life.

Very often an Amœba in the course of its wanderings comes in contact with a still smaller organism, such as a diatom (see Lesson XIV., Fig. 35) or a small infusor (see Lessons X.—XII.). When this happens the Amœba may be seen to extend itself round the lesser organism until the latter becomes sunk in its protoplasm in much the same way as a marble might be pressed into a lump of clay (Fig. 1, c, *a*). The diatom or other organism becomes in this way completely enclosed in a cavity or *food-vacuole* (*f. vac*), which also contains a small quantity of water necessarily included with the prey. The latter is taken in by the Amœba as food: so that another function performed by the animalcule is the *reception* of food, the first step in the process of *nutrition*. It is to be noted that the reception of food takes place in a particular way, viz. by *ingestion*—*i.e.* it is enclosed raw and entire in the living protoplasm. It has been noticed that Amœba usually ingests at its hinder end—that is, the end directed backwards in progression.

Having thus ingested its prey, the Amœba continues its course, when, if carefully watched, the swallowed organism will be seen to undergo certain changes. Its protoplasm is slowly dissolved; if it contains chlorophyll—the green colouring matter of plants—this is gradually turned to brown; and finally nothing is left but the case or cell-wall in which many minute organisms, such as diatoms, are enclosed. Finally, the Amœba, as it creeps slowly on, leaves this empty cell-wall behind, and thus gets rid of what it has no further

use for. It is thus able to *ingest* living organisms as food; to dissolve or *digest* their protoplasm; and to *egest* or get rid of any insoluble materials they may contain. Note that all this is done without either ingestive aperture (mouth), digestive cavity (stomach), or egestive aperture (anus); the food is simply taken in by the flowing round it of protoplasm, digested as it lies enclosed in the protoplasm, and the useless part got rid of by the Amœba flowing away from it.

It has just been said that the protoplasm of the prey is dissolved or digested: we must now consider more particularly what this means.

The stomachs of the higher animals—ourselves, for instance—produce in their interior a fluid called *gastric juice*. When this fluid is brought into contact with albumen or any other proteid a remarkable change takes place. The proteid is dissolved and at the same time rendered diffusible, so as to be capable, like a solution of salt or sugar, of passing through an organic membrane (see p. 6). The diffusible proteids thus formed by the action of gastric juice upon ordinary proteids are called *peptones*: the transformation is effected through the agency of a constituent of the gastric juice called *pepsin*.

There can be little doubt that the protoplasm of Amœba is able to convert that of its prey into a soluble and diffusible form by the agency of some substance analogous to pepsin, and that the dissolved matters diffuse through the body of the Amœba until the latter is, as it were, soaked through and through with them. Under these circumstances the Amœba may be compared to a sponge which is allowed to absorb water, the sponge itself representing the living protoplasm, the water the solution of proteids which permeates it. It has been proved by experiment that proteids are the only class of food which Amœba can make use of: it is unable to

digest either starch or fat—two very important constituents of the food of the higher animals. Mineral matters must, however, be taken with the food in the form of a weak watery solution, since the water in which the animalcule lives is never absolutely pure.

The Amœba being thus permeated, as it were, with a nutrient solution, a very important process takes place. The elements of the solution, hitherto arranged in the form of peptones, mineral salts, and water, become rearranged in such a way as to form new particles of living protoplasm, which are deposited among the pre-existing particles. In a word, the food is *assimilated* or converted into the actual living substance of the Amœba.

One effect of this formation of new protoplasm is obvious: if nothing happens to counteract it, the Amœba must *grow*, the increase in size being brought about in much the same way as that of a heap of stones would be by continually thrusting new pebbles into the interior of the heap. This mode of growth—by the interposition of new particles among old ones—is called growth by *intussusception*, and is very characteristic of the growth of protoplasm. It is necessary to distinguish it, because there is another mode of growth which is characteristic of minerals and occurs also in some organized structures. A crystal of alum, for instance, suspended in a strong solution of the same substance, grows; but the increase is due to the deposition of successive layers on the surface of the original crystal, in much the same way as a candle might be made to grow by repeatedly dipping it into melted grease. This can be proved by colouring the crystal with logwood or some other dye before suspending it, when a gradually-increasing colourless layer will be deposited round the coloured crystal: if growth took place by intussusception we should have a gradual weakening

of the tint as the crystal increased in size. This mode of growth—by the deposition of successive layers—is called growth by *accretion*.

It is probable that the cyst of Amœba referred to above (p. 11) grows by accretion. Judging from the analogy of other organisms it would seem that, after rounding itself off, the surface of the sphere of protoplasm undergoes a chemical change resulting in the formation of a thin superficial layer of non-protoplasmic substance. The process is repeated, new layers being continually deposited within the old ones until the cell-wall attains its full thickness. The cyst is therefore a substance separated or *secreted* from the protoplasm; it is the first instance we have met with of a *product of secretion*.

From the fact that Amœba rarely attains a greater diameter than $\frac{1}{4}$ mm., it follows that something must happen to counteract the constant tendency to grow, which is one of the results of assimilation. We all know what happens in our own case: if we take a certain amount of exercise—walk ten miles or lift a series of heavy weights—we undergo a loss of substance manifested by a diminution in weight and by the sensation of hunger. Our bodies have done a certain amount of work, and have undergone a proportional amount of waste, just as a fire every time it blazes up consumes a certain weight of coal.

Precisely the same thing happens on a small scale with Amœba. Every time it thrusts out or withdraws a pseudopod, every time it contracts its vacuole, it does a certain amount of work—moves a definite weight of protoplasm through a given space. And every movement, however slight, is accompanied by a proportional waste of substance, a certain fraction of the protoplasm becoming oxidized, or in other words undergoing a process of low temperature combustion.

When we say that any combustible body is burnt what we usually mean is that it has combined with oxygen, forming certain products of combustion due to the chemical union of the oxygen with the substance burnt. For instance, when carbon is burnt the product of combustion is carbon dioxide or carbonic acid ($C + O_2 = CO_2$): when hydrogen is burnt, water ($H_2 + O = H_2O$). The products of the slow combustion which our own bodies are constantly undergoing are these same two bodies—carbon dioxide given off mainly in the air breathed out, and water given off mainly in the form of perspiration and urine—together with two compounds containing nitrogen, urea (CH_4N_2O) and uric acid ($C_5H_4N_4O_3$), both occurring mainly in the urine. In some animals urea and uric acid are replaced by other compounds such as guanin ($C_5H_5N_5O$), but it may be taken as proved that in all living things the products of combustion are carbon dioxide, water, and some nitrogenous substance of simpler constitution than proteids, and allied to the three just mentioned.

With this breaking down of proteids the vital activities of all organisms are invariably connected. Just as useful mechanical work may be done by the fall of a weight from a given height to the level of the ground, so the work done by the organism is a result of its complex proteids falling, so to speak, to the level of simpler substances. In both instances potential energy or energy of position is converted into kinetic or actual energy.

In the particular case under consideration we have to rely upon analogy and not upon direct experiment. We may, however, be quite sure that the products of combustion or waste matters of Amœba include carbon dioxide, water, and some comparatively simple (as compared with proteids) compound of nitrogen.

These waste matters or *excretory products* are given off partly from the general surface of the body, but partly, it would seem, through the agency of the contractile vacuole. It appears that the water taken in with the food, together in all probability with some of that formed by oxidation of the protoplasm, makes its way to the vacuole, and is expelled by its contraction. We have here another function, performed by Amœba, that of *excretion*, or the getting rid of waste matters.

In this connection the reader must be warned against a possible misunderstanding arising from the fact that the word excretion is often used in two senses. We often hear, for instance, of solid and liquid "excreta." In Amœba the solid excreta, or more correctly *fæces*, consist of such things as the indigestible cell-walls, starch grains, &c., of the organisms upon which it feeds; but the rejection of these is no more a process of excretion than the spitting out of a cherry-stone, since they are simply parts of the food which have never been assimilated—never formed part and parcel of the organism. True excreta, on the other hand, are invariably products of the waste or decomposition of protoplasm.[1]

The statement just made that the protoplasm of Amœba constantly undergoes oxidation presupposes a constant supply of oxygen. The water in which the animalcule lives invariably contains that gas in solution: on the other hand, as we have seen, the protoplasm is continually forming carbon dioxide. Now when two gases are separated from one another by a porous partition, an interchange takes place between them, each diffusing into the space occupied by the

[1] In the higher animals the distinction between excreta and fæces is complicated by the fact that the latter always contain true excretory products derived from the epithelium of the intestine and its glands.

other. The same process of gaseous diffusion is continually going on between the carbon dioxide in the interior of Amœba and the oxygen in the surrounding water, the protoplasm acting as the porous partition. In this way the carbon dioxide is got rid of, and at the same time a supply of oxygen is obtained for further combustion.

The taking in of oxygen might be looked upon as a kind of feeding process, the food being gaseous instead of solid or liquid, just as we might speak of "feeding" a fire both with coals and with air. Moreover, as we have seen, the giving out of carbon dioxide is a process of excretion. It is, however, usual and convenient to speak of this process of exchange of gases as *respiration* or breathing, which is therefore another function performed by the protoplasm of Amœba.

The oxidation of protoplasm in the body of an organism, like the combustion of wood or coal in a fire, is accompanied by an *evolution of heat*. That this occurs in Amœba cannot be doubted, although it has never been proved. The heat thus generated is, however, constantly being lost to the surrounding water, so that the temperature of Amœba, if we could but measure it, would probably be found, like that of a frog or a fish, to be very little if at all above that of the medium in which it lives.

We thus see that a very elaborate series of chemical processes is constantly going on in the interior of Amœba. These processes are divisible into two sets: those which begin with the digestion of food and end with the manufacture of living protoplasm, and those which have to do with the destruction of protoplasm and end with excretion.

The whole series of processes are spoken of collectively as *metabolism*. We have, first of all, digested food diffused through the protoplasm and finally converted into fresh

living protoplasm: this is the process of *constructive metabolism* or *anabolism*. Next we have the protoplasm, gradually breaking down and undergoing conversion into excretory products: this is the process of *destructive metabolism* or *katabolism*. There can be little doubt that both are processes of extreme complexity: it seems probable that after the food is once dissolved there ensues the successive formation of numerous bodies of gradually increasing complexity (*anabolic mesostates* or *anastates*), culminating in protoplasm; and that the protoplasm, when once formed, is decomposed into a series of substances of gradually diminishing complexity (*katabolic mesostates* or *katastates*), the end of the series being formed by the comparatively simple products of excretion. The granules in the endosarc are probably to be looked upon as various mesostates imbedded in the protoplasm proper.

Living protoplasm is thus the most unstable of substances; it is never precisely the same thing for two consecutive seconds: it "decomposes but to recompose," and recomposes but to decompose; its existence, like that of a waterfall or a fountain, depends upon the constant flow of matter into it and away from it.

It follows from what has been said that if the income of an Amœba, *i.e.*, the total weight of substances taken in (food *plus* oxygen *plus* water) is greater than its expenditure or the total weight of substances given out (fæces *plus* excreta proper *plus* carbon dioxide) the animalcule will grow: if less it will dwindle away: if the two are equal it will remain of the same weight or in a state of physiological equilibrium.

We see then that the fundamental condition of existence of the individual Amœba is that it should be able to form new protoplasm out of the food supplied to it. But some-

thing more than this is necessary. Amœbæ are subject to all sorts of casualties; they may be eaten by other organisms or the pool in which they live may be dried up; in one way or another they are constantly coming to an end. From which it follows that if the race of Amœbæ is to be preserved there must be some provision by which the individuals composing it are enabled to produce new individuals. In other words Amœba must, in addition to its other functions, perform that of *reproduction*.

An Amœba reproduces itself in a very simple way. The nucleus first divides into two: then the whole organism elongates, the two nuclei at the same time travelling away from one another: next a furrow appears across the middle of the drawn-out body between the nuclei (Fig. 1, I; fig. 2, C, D): the furrow deepens until finally the animalcule separates into two separate Amœbæ (Fig. 2, E), which henceforward lead an independent existence.

This, the simplest method of reproduction known, is called *simple* or *binary fission*. Notice how strikingly different it is from the mode of multiplication with which we are familiar in the higher animals. A fowl, for instance, multiplies by laying eggs at certain intervals, in each of which, under favourable circumstances, and after a definite lapse of time, a chick is developed: moreover, the parent bird, after continuing to produce eggs for a longer or shorter time, dies. An Amœba, on the other hand, simply divides into two Amœbæ, each exactly like itself, and in doing so ceases to exist as a distinct individual. Instead of the successive production of offspring from an ultimately dying parent, we have the simultaneous production of offspring by the division of the parent, which does not die, but becomes simply merged in its progeny. There can be no better instance of the fact that reproduction is discontinuous growth.

From this it seems that an Amœba, unless suffering a violent death, is practically immortal, since it divides into two completely organised individuals, each of which begins life with half of the entire body of its parent, there being therefore nothing left of the latter to die. It is possible, however, judging from the analogy of the Infusoria (see Lesson X.) that such organisms as Amœba cannot go on multiplying indefinitely by simple fission, and that occasionally two individuals come into contact and undergo complete fusion. A *conjugation* of this kind has been observed in Amœba, but has been more thoroughly studied in other forms (see Lessons III., X., XII.). Whether it is a necessary condition of continued existence in our animalcule or not, it appears certain that "death has no place as a natural recurrent phenomenon" in that organism.

Amœba may also be propagated artificially. If a specimen is cut into pieces each fragment is capable of developing into a complete animalcule provided it contains a portion of nuclear matter, but not otherwise. From this it is obvious that the nucleus exerts an influence of the utmost importance over the vital processes of the organism.

If an Amœba does happen to be killed and to escape being eaten it will undergo gradual decomposition, becoming converted into various simple substances of which carbon dioxide, water, and ammonia are the chief. (See p. 91.)

In conclusion, a few facts may be mentioned as to the conditions of life of Amœba—the circumstances under which it will live or die, flourish or otherwise.

In the first place, it will live only within certain limits of temperature. In moderately warm weather the temperature to which it is exposed may be taken as about 15° C. If gradually warmed beyond this point the movements at first

show an increased activity, then become more and more sluggish, and at about 30°—35° C. cease altogether, recommencing, however, when the temperature is lowered. If the heating is continued up to about 40° C. the animalcule is killed by the coagulation of its protoplasm (see p. 5): it is then said to suffer *heat-rigor* or death-stiffening produced by heat. Similarly when it is cooled below the ordinary temperature the movements become slower and slower, and at the freezing point (0° C.) cease entirely. But freezing, unlike over-heating, does not kill the protoplasm, but only renders it temporarily inert; on thawing the movements recommence. We may therefore distinguish an *optimum* temperature at which the vital actions are carried on with the greatest activity; *maximum* and *minimum* temperatures above and below which respectively they cease; and an *ultra-maximum* temperature at which death ensues. There is no definite ultra-minimum temperature known in the case of Amœba.

The quantity of water present in the protoplasm—as water of organization (see p. 5)—is another matter of importance. The water in which Amœba lives always contains a certain percentage of salts in solution, and the protoplasm is affected by any alteration in the density of the surrounding medium; for instance, by replacing it by distilled water and so reducing the density, or by adding salt and so increasing it. The addition of common salt (sodium chloride) to the amount of two per cent. causes Amœba to withdraw its pseudopods and undergo a certain amount of shrinkage: it is then said to pass into a condition of *dry-rigor*. Under these circumstances it may be restored to its normal condition by adding a sufficient proportion of water to bring back the fluid to its original density.

In this connection it is interesting to notice that the dele-

terious effects of an excess of salt are produced only when the salt is added suddenly. By the very gradual addition of sodium chloride Amœbæ have been brought to live in a four per cent. solution, *i.e.*, one twice as strong as would, if added suddenly, produce dry-rigor.

From what has been said above on the subject of respiration (p. 17) it follows that free oxygen is necessary for the existence of Amœba. Light, on the other hand, appears to be unnecessary, amœboid movements having been shown to go on actively in darkness.

LESSON II

HÆMATOCOCCUS

THE rain-water which collects in puddles, open gutters, &c., is frequently found to have a green or red colour. The colour is due to the presence of various organisms —plants or animals—one of the commonest of which is called *Hæmatococcus* (or as it is sometimes called *Sphærella* or *Protococcus*) *pluvialis*.

Like Amœba, Hæmatococcus is so small as to require a high power for its examination. Magnified three or four hundred diameters it has the appearance (Fig. 3, A) of an ovoidal body, somewhat pointed at one end, and of a bright green colour, more or less flecked with equally bright red.

Like Amœba, moreover, it is in constant movement, but the character of the movement is very different in the two cases. An active Hæmatococcus is seen to swim about the field of the microscope in all directions and with considerable apparent rapidity. We say *apparent* rapidity because the rate of progression is magnified to the same extent as the organism itself, and what appears a racing speed under the microscope is actually a very slow crawl when divided by 300. It has been found that such organisms as Hæmatococcus travel at the rate of one foot in from a quarter of an hour to an hour: or, to express

the fact in another and fairer way, that they travel a distance equal to two and a half times their own diameter in one second. In swimming the pointed end is always directed

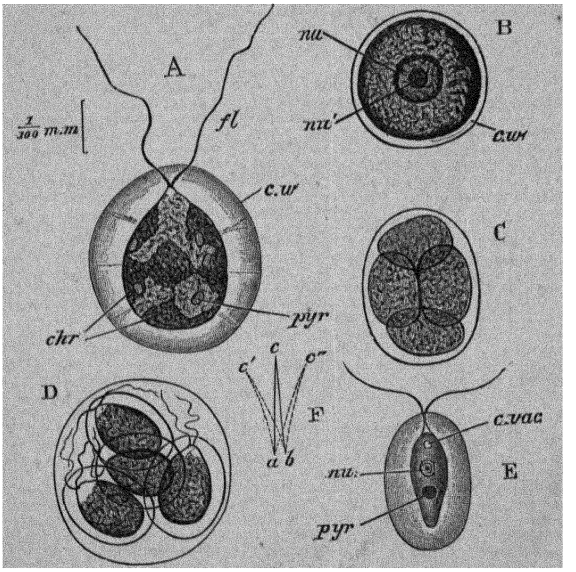

FIG. 3.—A. *Hæmatococcus pluvialis*, motile phase. Living specimen, showing protoplasm with chromatophore (*chr*) and pyrenoids (*pyr*), cell-wall (*c. w*) connected to cell-body by protoplasmic filaments, and flagella (*fl.*). The scale to the left applies to Figs. A—D.

B. Resting stage of the same, showing nucleus (*nu*) with "nucleolus" (*nu'*), and thick cell-wall (*c. w*) in contact with protoplasm.

C. The same, showing division of the cell-body in the resting stage into four daughter-cells.

D. The same, showing the development of flagella and detached cell-wall by the daughter-cells before their liberation from the enclosing mother-cell-wall.

E. *Hæmatococcus lacustris*, showing nucleus (*nu*), single large pyrenoid (*pyr*), and contractile vacuole (*c. vac*).

F. Diagram illustrating the movement of a flagellum: *ab*, its base; *c*, *c'*, *c''*, different positions assumed by its apex. (E, after Butschli.)

forwards and the forward movement is accompanied by a rotation of the organism upon its longer axis.

Careful watching shows that the outline of a swimming Hæmatococcus does not change, so that there is evidently no protrusion of pseudopods, and at first the cause of the movement appears rather mysterious. Sooner or later, however, the little creature is sure to come to rest, and there can then be seen projecting from the pointed end two excessively delicate colourless threads (Fig. 3, A, *fl*), each about half as long again as the animalcule itself: these are called *flagella* or sometimes *cilia*.[1] In a Hæmatococcus which has come to rest these can often be seen gently waving from side to side: when this slow movement is exchanged for a rapid one the whole organism is propelled through the water, the flagella acting like a pair of extremely fine and flexible fins or paddles. Thus the movement of Hæmatococcus is not *amœboid*, *i.e.*, produced by the protrusion and withdrawal of pseudopods, but is *ciliary*, *i.e.*, due to the rapid vibration of cilia or flagella.

The flagella are still more clearly seen by adding a drop of iodine solution to the water: this immediately kills and stains the organism, and the flagella are seen to take on a distinct yellow tint. By this and other tests it is shown that Hæmatococcus, like Amœba, consists of protoplasm, and that the flagella are simply filamentous processes of the protoplasm.

It was mentioned above that in swimming the pointed end

[1] The word *cilium* is sometimes used as a general term to include any delicate vibratile process of protoplasm: often, however, it is used in a restricted sense for a rhythmically vibrating thread, of which each cell bears a considerable number (see Fig. 8, E, and Fig. 20); a flagellum is a cilium having a whip-lash-like movement, each cell bearing only a limited number—one or two, or occasionally as many as four.

with the flagella goes first; this may therefore be distinguished as the anterior extremity, the opposite or blunt end being posterior. So that as compared with Amœba, Hæmatococcus exhibits a *differentiation of structure:* an anterior and a posterior end can be distinguished, and a part of the protoplasm is differentiated or set apart as flagella.

The green colour of the body is due to the presence of a special pigment called *chlorophyll*, the substance to which the colour of leaves is due. That this is something quite distinct from the protoplasm may be seen by treatment with alcohol, which simply kills and coagulates the protoplasm, but completely dissolves out the chlorophyll, producing a clear green solution. The solution, although green by transmitted light, is red under a strong reflected light, and is hence *fluorescent:* when examined through the spectroscope it has the effect of absorbing the whole of the blue and violet end of the spectrum as well as a part of the red. The red colour which occurs in so many individuals, sometimes entirely replacing the green, is due to a colouring matter closely allied in its properties to chlorophyll and called *hæmatochrome*.

At first sight the chlorophyll appears to be evenly distributed over the whole body, but accurate examination under a high power shows it to be lodged in a structure called a *chromatophore* (Fig. 3, A, *chr*), which forms a layer immediately beneath the surface, and in this case is relatively large and urn-shaped. It consists of a protoplasmic substance impregnated with chlorophyll.

After solution of the chlorophyll with alcohol a nucleus (B, *nu.*) can be made out; like the nucleus of Amœba it is stained by iodine, magenta, &c. Other bodies which might easily be mistaken for nuclei are also visible in the living

organism. These are small ovoidal structures (A, *pyr.*), with clearly defined outlines occurring in varying numbers in the chromatophores. When treated with iodine they assume a deep, apparently black but really dark blue, colour. The assumption of a blue colour with iodine is the characteristic test of the well-known substance *starch*, as can be seen by letting a few drops of a weak solution of iodine fall upon some ordinary washing starch. The bodies in question have been found to consist of a proteid substance covered with a layer of starch, and are called *pyrenoids*. Starch itself is a definite chemical compound belonging to the group of *carbohydrates*, *i.e.*, bodies containing the elements carbon, hydrogen, and oxygen: its formula is $C_6H_{10}O_5$.

In Hæmatococcus pluvialis there is usually said to be no contractile vacuole, but in another species, *H. lacustris*, this structure is present as a minute space near the anterior or pointed end (Fig. 3, E, *c. vac*),

There is still another characteristic structure to which no reference has yet been made. This appears at the first view something like a delicate haze around the red or green body, but by careful focusing is seen to be really an extremely thin globular shell (A, *c.w.*) composed of some colourless transparent material and separated, by a space containing water, from the body, to which it is connected by very delicate radiating strands of protoplasm. It is perforated by two extremely minute apertures for the passage of the flagella. Obviously we may consider this shell as a cyst or *cell-wall* differing from that of an encysted Amœba (Fig. 1, D) in not being in close contact with the protoplasm.

A more important difference, however, lies in its chemical composition. The cyst or cell-wall of Amœba, as stated in the preceding lesson (p. 11) is very probably nitrogenous:

that of Hæmatococcus, on the other hand, is formed of a carbohydrate called *cellulose*, allied in composition to starch, sugar, and gum, and having the formula $C_6 H_{10} O_5$. Many vegetable substances, such as cotton, consist of cellulose, and wood is a modification of the same compound. Cellulose is stained yellow by iodine, but iodine and sulphuric acid together turn it blue, and a similar colour is produced by a solution of iodine and potassium iodide in zinc chloride known as Schulze's solution. These tests are quite easily applied to Hæmatococcus: the protoplasm stains a deep yellowish-brown, and around it is seen a sort of blue cloud due to the stained and partly-dissolved cell-wall.

It has been stated that in stagnant water in which it has been cultivated for a length of time Hæmatococcus sometimes assumes an amœboid form. In any case, after leading an active existence for a longer or shorter time it comes to rest, loses its flagella, and throws around itself a thick cell-wall of cellulose (Fig. 3, B), thus becoming encysted. So that, as in Amœba, there is an alternation of an active or motile with a stationary or resting condition.

In the matter of nutrition the differences between Hæmatococcus and Amœba are very marked and indeed fundamental. As we have seen, Hæmatococcus has no pseudopods, and therefore cannot take in solid food after the manner of Amœba: moreover, even in its active condition it is usually surrounded by an imperforate cell-wall, which of course quite precludes the possibility of ingestion. As a matter of observation, also, however long it is watched it is never seen to *feed* in the ordinary sense of the word. Nevertheless it must take in food in some way or other, or the decomposition of its protoplasm would soon bring it to an end.

Hæmatococcus lives in rain-water. This is never pure water, but always contains certain mineral salts in solution, especially nitrates, ammonia salts, and often sodium chloride or common table salt. These salts, being crystalloids, can and do diffuse into the water of organization of the animalcule, so that we may consider its protoplasm to be constantly permeated by a very weak saline solution, the most important elements contained in which are oxygen, hydrogen, nitrogen, potassium, sodium, calcium, sulphur, and phosphorus. It must be remarked, however, that the diffusion of these salts does not take place in the same uniform manner as it would through parchment or other dead membrane. The living protoplasm has the power of determining the extent to which each constituent of the solution shall be absorbed.

If water containing a large quantity of Hæmatococcus is exposed to sunlight, minute bubbles are found to appear in it, and these bubbles, if collected and properly tested, are found to consist largely of oxygen. Accurate chemical analysis has shown that this oxygen is produced by the decomposition of the carbon dioxide contained in solution in rain-water, and indeed in all water exposed to the air, the gas, which is always present in small quantities in the atmosphere, being very soluble in water.

As the carbon dioxide is decomposed in this way, its oxygen being given off, it is evident that its carbon must be retained. As a matter of fact it is retained by the organism but not in the form of carbon; in all probability a double decomposition takes place between the carbon dioxide absorbed and the water of organization, the result being the liberation of oxygen in the form of gas and the simultaneous production of some extremely simple form of carbohydrate, *i.e.* some compound of carbon, hydrogen, and oxygen,

with a comparatively small number of atoms to the molecule.

The next step seems to be that the carbohydrate thus formed unites with the ammonia salts or the nitrates absorbed from the surrounding water, the result being the formation of some comparatively simple nitrogenous compound, probably belonging to the class of amides, one of the best known of which – asparagin — has the formula $C_4H_8N_2O_3$. Then further combinations take place, substances of greater and greater complexity are produced, sulphur from the absorbed sulphates enters into combination, and proteids are formed. From these, finally, fresh living protoplasm arises.

From the foregoing account, which only aims at giving the very briefest outline of a subject as yet imperfectly understood, it will be seen that, as in Amœba, the final result of the nutritive process is the manufacture of protoplasm, and that this result is attained by the formation of various substances of increasing complexity or anastates (see p. 18). But it must be noted that the steps in this process of constructive metabolism are widely different in the two cases. In Amœba we start with living protoplasm—that of the prey —which is killed and broken up into diffusible proteids, these being afterwards re-combined to form new molecules of the living protoplasm of Amœba. So that the food of Amœba is, to begin with, as complex as itself, and is first broken down by digestion into simpler compounds, these being afterwards re-combined into more complex ones. In Hæmatococcus, on the other hand, we start with extremely simple compounds, such as carbon dioxide, water, nitrates, sulphates, &c. Nothing which can be properly called digestion, *i.e.*, a breaking up and dissolving of the food, takes place, but its various constituents are combined into sub-

stances of gradually increasing complexity, protoplasm, as before, being the final result.

To express the matter in another way: Amœba can only make protoplasm out of proteids already formed by some other organism: Hæmatococcus can form it out of simple liquid and gaseous inorganic materials.

Speaking generally, it may be said that these two methods of nutrition are respectively characteristic of the two great groups of living things. Animals require solid food containing ready-made proteids, and cannot build up their protoplasm out of simpler compounds. Green plants, *i.e.*, all the ordinary trees, shrubs, weeds, &c., take only liquid and gaseous food, and build up their protoplasm out of carbon dioxide, water, and mineral salts. The first of these methods of nutrition is conveniently distinguished as *holozoic*, or wholly-animal, the second as *holophytic*, or wholly-vegetal.

It is important to note that only those plants or parts of plants in which chlorophyll is present are capable of holophytic nutrition. Whatever may be the precise way in which the process is effected, it is certain that the decomposition of carbon dioxide which characterizes this form of nutrition is a function of chlorophyll, or to speak more accurately, of chromatophores, since there is reason for thinking that it is the protoplasm of these bodies and not the actual green pigment which is the active agent in the process.

Moreover, it must not be forgotten that the decomposition of carbon dioxide is carried on only during daylight, so that organisms in which holophytic nutrition obtains are dependent upon the sun for their very existence. While Amœba derives its energy from the breaking down of the proteids in its food (see p. 15), the food of Hæmatococcus is too simple to serve as a source of energy, and it is only by the help of sunlight that the work of constructive metabolism

can be carried on. This may be expressed by saying that Hæmatococcus, in common with other organisms containing chlorophyll, is supplied with kinetic energy (in the form of light or radiant energy) directly by the sun.

As in Amœba, destructive metabolism is constantly going on, side by side with constructive. The protoplasm becomes oxidized, water, carbon dioxide, and nitrogenous waste matters being formed and finally got rid of. Obviously then, absorption of oxygen must take place, or in other words, respiration must be one of the functions of the protoplasm of Hæmatococcus as of that of Amœba. In many green, *i.e.*, chlorophyll-containing, plants, this has been proved to be the case; respiration, *i.e.*, the taking in of oxygen and giving out of carbon dioxide, is constantly going on, but during daylight is obscured by the converse process—the taking in of carbon dioxide for nutritive purposes and the giving out of the oxygen liberated by its decomposition. In darkness, when this latter process is in abeyance, the occurrence of respiration is more readily ascertained.

Owing to the constant decomposition, during sunlight, of carbon dioxide, a larger volume of oxygen than of carbon dioxide is evolved; and if an analysis were made of all the ingesta of the organism (carbon dioxide *plus* mineral salts *plus* respiratory oxygen) they would be found to contain less oxygen than the egesta (oxygen from decomposition of carbon dioxide *plus* water, excreted carbon dioxide and nitrogenous waste); so that the nutritive process in Hæmatococcus is, as a whole, a process of deoxidation. In Amœba, on the other hand, the ingesta (food *plus* respiratory oxygen) contain more oxygen than the egesta (fæces *plus* carbon dioxide, water, and nitrogenous excreta), the nutritive process being therefore on the whole one of oxidation. This difference is, speaking broadly, character-

istic of plants and animals generally; animals, as a rule, take in more free oxygen than they give out, while green plants always give out more than they take in.

But destructive metabolism is manifested not only in the formation of waste products, but in that of substances, simpler than protoplasm, which remain an integral part of the organism, viz., cellulose and starch. The cell-wall is probably formed by the conversion of a thin superficial layer of protoplasm into cellulose, the cyst attaining its final thickness by frequent repetition of the process (see p. 14). The starch of the pyrenoids is apparently formed by a similar process of decomposition or destructive metabolism of protoplasm, growth taking place, in both instances, by accretion and not by intussusception.

We see then that destructive metabolism may result in the formation of (*a*) *waste products* and (*b*) *plastic products*, the former being got rid of as of no further use, while the latter remain an integral part of the organism.

Let us now turn once more to the movements of Hæmatococcus, and consider in some detail the manner of their performance.

Each flagellum (Fig. 3, A, *fl*) is a thread of protoplasm of uniform diameter except at its distal or free end where it tapers to a point. The lashing movements are brought about by the flagellum bending successively in different directions; for instance, if in Fig. 3 F, *abc* represents it in the position of rest, *abc'* will show the form assumed when it is deflected to the left, and *abc''* when the bending is towards the right. In the position *abc* the two sides *ab*, *ac* are obviously equal to one another, but in the flexed positions it is equally obvious that the concave sides *ac'*, *bc''* are shorter than the convex sides *bc'*, *ac''*; in other words, as

the flagellum bends to the left side *ac* becomes shortened, as it bends to the right the side *bc*.

This may be otherwise expressed by saying that in bending to the left the side *ac* contracts (see p. 10), in bending to the right the side *bc*, or that the movement is performed by the alternate contraction of opposite sides of the flagellum.

Thus the ciliary movement of Hæmatococcus, like the amœboid movement of Amœba, is a phenomenon of *contractility*. Imagine an Amœba to draw in all its pseudopods but two, and to protrude these two until they became mere threads; imagine further these threads to contract regularly and rapidly instead of irregularly and slowly; the result would be the substitution of pseudopods by flagella, *i.e.*, of temporary slow-moving processes of protoplasm by permanent rapidly-moving ones.

To put the matter in another way: in Amœba the function of contractility is performed by the whole organism; in Hæmatococcus it is discharged by a small part only, viz., the flagella, the rest of the protoplasm being incapable of movement. We have therefore in Hæmatococcus a *differentiation of structure* accompanied by a *differentiation of function* or *division of physiological labour*.

The expression "division of physiological labour" was invented by the great French physiologist, Henri Milne-Edwards, to express the fact that a sort of rough correspondence exists between lowly and highly organized animals and plants on the one hand, and lowly and highly organized human societies on the other. In primitive communities there is little or no division of labour: every man is his own butcher, baker, soldier, doctor, &c., there is no distinction between "classes" and "masses," and each individual is to a great extent independent of all the rest. Whereas in

complex civilized communities society is differentiated into politicians, soldiers, professional men, mechanics, labourers, and so on, each class being to a great extent dependent on every other. This comparison of an advanced society with a high organism is at least as old as Æsop, who gives expression to it in the well-known fable of "the Belly and Members."

We see the very first step towards a division of labour in the minute organism now under consideration. If we could cut off a pseudopod of Amœba the creature would be little or none the worse, since every part would be capable of sending off similar processes, and so movement would be in no way hindered. But if we could amputate the flagella of Hæmatococcus its movements would be absolutely stopped.

Hæmatococcus multiplies only in the resting condition (p. 28, and Fig. 3, B); as in Amœba its protoplasm undergoes simple or binary fission, but with the peculiarity that the process is immediately repeated, so that four *daughter-cells* are produced within the single mother-cell-wall (Fig. 3 C). By the rupture of the latter the daughter-cells are set free in the ordinary motile form; sometimes they acquire their flagella and detached cell-wall before making their escape (D).

Under certain circumstances the resting form divides into eight or even more daughter-cells, and these when liberated are found to be smaller than the ordinary motile form, and to have no cell-wall. Hæmatococcus is therefore *dimorphic*, *i.e.*, occurs, in the motile condition, under two distinct forms: the larger or ordinary form with detached cell-wall is called a *megazooid*, the smaller form without a cell-wall a *microzooid*.

LESSON III

HETEROMITA

WHEN animal or vegetable matter is placed in water and allowed to stand at the ordinary temperature, the well known process called decomposition sooner or later sets in, the water becoming turbid and acquiring a bad smell. A drop of it examined under the microscope is then found to teem with minute organisms. To one of these, called "the Springing Monad," or in the language of zoology, *Heteromita rostrata*, we must now direct our attention; it is found in infusion of cod's head which has been allowed to stand for two or three months.

Heteromita (Fig. 4, A) is considerably smaller than either Amœba or Hæmatococcus, being only $\frac{1}{120}$ mm. ($\frac{1}{3000}$ inch) in average length. It has a certain resemblance in general form to Hæmatococcus, being somewhat ovoidal and pointed at one end. Like Hæmatococcus also it has two flagella, but only one of these (*fl.* 1) proceeds from its beak-like anterior end and is directed forwards as the creature swims; the other (*fl.* 2) springs a short distance from the beak, and in the ordinary swimming position is trailed after the organism as in A^2 and F^4. Thus in Heteromita, besides an anterior and a posterior end, we may distinguish a *ventral*

surface which is directed downwards in the ordinary position, and bears the second or trailing flagellum, and an opposite or *dorsal* surface directed upwards.

Often instead of swimming freely in the fluid a Heteromita is found anchored as it were to a bit of the decomposing substance by its ventral flagellum as in A[1]. Under these circumstances it is in constant movement, springing backwards and forwards by alternately coiling and uncoiling the attached ventral flagellum. The general character of the movement will be readily understood from the figure, in which A[1] shows the monad with coiled flagellum, A[2] after it has sprung forward to the full extent of the flagellum. It is from this curious habit that the name "springing monad" is derived.

Towards the posterior end of the body is a nucleus (*nu*), and at the anterior end a contractile vacuole (*c. vac*). There is no trace of an investing membrane or cell-wall, and the protoplasm is colourless. Also, as is invariably the case with organisms devoid of chlorophyll, there is no starch.

In considering the nutrition of Heteromita it is necessary, first of all, to take into consideration the precise nature of its surroundings. It lives, as already stated, in decomposing infusions of animal matter. Such infusions contain proteids in solution, in part split up by the process of decomposition into simpler compounds some of which are diffusible; this process is due, as we shall see hereafter (Lesson VIII.), to the action of the minute organisms known as Bacteria, which are always present in vast numbers in putrescent substances.

As Heteromita contains no chlorophyll its nutrition is obviously not holophytic. Observation seems to show pretty conclusively that it is not holozoic; apart from the

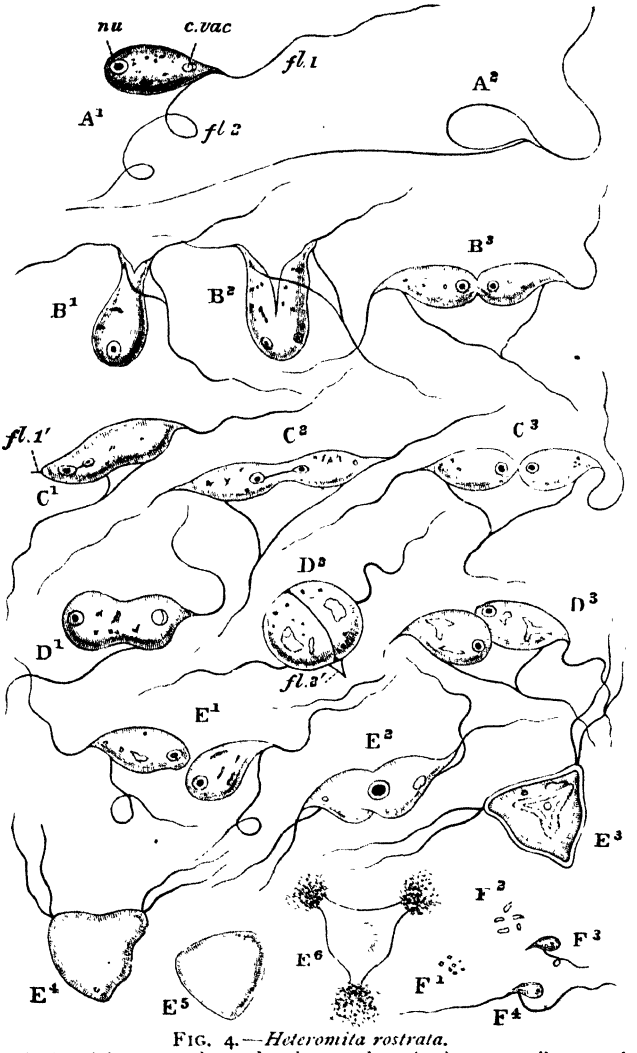

FIG. 4.—*Heteromita rostrata.*

A[1], the living organism, showing nucleus (*nu*), contractile vacuole

(*c. vac*), anterior flagellum (*fl.* 1), and coiled ventral flagellum (*fl.* 2) by which the organism is anchored; A^2 shows the position at the forward limit of the spring, the ventral flagellum being fully extended.

B^1—B^3, three stages in the longitudinal fission of the anchored form.

C^1—C^3. Three stages in the transverse fission of the same: *fl.* 1^1. rudiment of newly formed anterior flagellum.

D^1—D^3, three stages in the fission of the free-swimming form: *fl.* 2^1, rudiment of the newly-formed ventral flagella.

E^1, free-swimming and anchored forms about to conjugate: E^2, commencement of conjugation: E^3, E^4, two stages in the development of the zygote: E^5, the fully formed zygote: E^6, dehiscence of the zygote and emission of spores.

F^1—F^4, four stages in the development of the spores.

(After Dallinger.)

fact that it possesses neither mouth nor pseudopods, examples have been kept under observation for hours together by trained microscopists, and have never been observed to ingest the bacteria or other particles, dead or alive, contained in the fluid. There remains only one way in which nutrition can take place, namely, by absorption of the proteids and other nutrient substances in the solution, *i.e.*, by these substances diffusing into the water of organisation of the monad. Whether the proteids are rendered diffusible by the process of decomposition alone, *i.e.*, by the action of bacteria (see p. 91), or whether a kind of surface digestion takes place, the protoplasm of Heteromita converting the proteids in immediate contact with it into peptones or allied compounds, is not certain.

Thus Heteromita feeds neither by taking solid proteinaceous food into its interior (holozoic nutrition) nor by decomposing carbon dioxide and combining the carbon with water and mineral salts (holophytic nutrition), but by absorbing decomposing proteids and other nutrient substances in the liquid form; this is the *saprophytic* mode of nutrition. It will be seen that the main difference between saprophytic and holozoic nutrition is that in the former digestion, *i.e.*, the process of rendering food-stuffs soluble and diffusible,

takes place outside the body so that constructive metabolism can begin at once.

It is worthy of notice that while the process of feeding is strictly intermittent in Amœba, which takes in food at irregular intervals, and largely intermittent in Hæmatococcus, in which the decomposition of carbon dioxide takes place only during daylight, in Heteromita it is continuous, the organism living in a solution of putrefying proteids which it is constantly absorbing. It may be said to live immersed in an immense cauldron of broth which it is for ever imbibing, not by its mouth, for it has none, but by the whole surface of its body.

Respiration and excretion probably take place in the same manner as in Amœba. It has been shown that the optimum temperature for saprophytic monads is about 18° C., the ultra-maximum or thermal death-point about 60° C. But it is an interesting fact that by very slowly increasing the temperature, Dr. Dallinger was able in the course of several months to accustom some of these forms—not Heteromita itself but closely allied genera—to live at a temperature exceeding 68° C.

The ordinary method of reproduction is by simple fission, the process affecting not only the body but the flagella as well. In Fig. 4, B,[1] the commencement of fission is shown; the anterior flagellum has undergone complete longitudinal division, while the split has extended only about a third of the length of the body and ventral flagellum. In B[2] the process has gone further, and in B[3] the products of division are on the point of separating.

More frequently, however, fission instead of being longitudinal, *i.e.*, in the direction of the long axis of the monad, is transverse, *i.e.*, at right angles to the long axis. This process is shown in C[1]—C[3], and is seen to differ from that described in the preceding paragraph in the cir-

cumstance that the anterior flagellum of the parent form is unaffected, and becomes without alteration the anterior flagellum of one of the daughter-forms—that to the right in the figures. The anterior flagellum of the other product of division—that to the left—is a new structure formed as an outgrowth from the body: its commencement is shown in C^1, *fl.* 1'.

These two modes of fission—longitudinal and transverse—both occur in the anchored form of Heteromita, *i.e.*, in individuals attached by the ventral flagellum. The free-swimming form presents a third variety of the process. It comes to rest, loses its regular outline (D^1) becoming almost amœboid in form and finally (D^2) globular. Division then takes place: the flagella of the parent become each the anterior flagellum of one of the daughter-cells (compare D^1, D^2, and D^3), while their ventral flagella are formed by the splitting of a little outgrowth of the dividing body (D^2, *fl.* 2').

As in Amœba fission is invariably preceded by division of the nucleus.

But in Heteromita fission is not the only mode of reproduction. Under certain circumstances a free-swimming form approaches an anchored form, and applies itself to it in such a way that the posterior ends of the two are in contact (E^1). The two individuals then fuse with one another as completely as two drops of gum on a plate unite when brought into contact. Fusion of the nuclei also takes place, and there is formed an irregular body (E^2) with a single nucleus and with two flagella at each end. This swims about freely, and as it does so the last trace of distinction between the two monads of which it is formed is lost, and a triangular form is assumed (E^3), the two pairs of flagella being situated at two of the angles. Still later the protoplasm of this triangular body loses all trace of nucleus, granules, &c., and becomes perfectly clear (E^4): then it comes to rest and loses its flagella, appearing as a clear, homogeneous, three-cornered sac with slightly convex sides (E^5). This body, formed by the *conjugation* of the two monads, is called a *zygote*, the two conjugating individuals being distinguished as *gametes*.

The zygote remains quiescent for some time, and then, after undergoing wave-like movements of its surface, bursts at its three angles (E[6]), its contents escaping in the form of granules called *spores*, so minute as to be barely visible even under the highest powers of the best modern microscopes. They are formed by the protoplasm of the zygote dividing into an immense number of separate masses, a process known as *multiple fission*.

Carefully watched, these almost ultra-microscopic particles (F[1]) are found to grow into clear visibility and to take on a distinctly oval shape (F[2]). Still increasing in size they develop a ventral flagellum (F[3]) which is at first quite quiescent: finally, the pointed end sends out a process which becomes an anterior flagellum (F[4]). The spore has now become a Heteromita resembling the parent form in all but size. As growth proceeds a nucleus becomes apparent. All analogy leads us to believe that this is not a new structure, but that the multiple fission of the protoplasm of the zygote is preceded by the multiple fission of its nucleus, each spore having thus its own ultra-microscopic nucleus from the very first.

It will be seen that this mode of multiplication following conjugation differs from ordinary multiplication by fission in that it requires the co-operation of two individuals which undergo complete fusion. As we shall see more plainly later on (Lessons XV., XVI.) conjugation leads to the simplest case of *sexual reproduction*, differing from the sexual reproduction of the higher organisms in that the two conjugating bodies or gametes are each an entire individual, and in the further circumstance that the gametes resemble one another in form and size, so that there is no distinction of sex,[1] but each takes an equal and similar share in the production of

[1] It might perhaps be allowable to consider the active, free-swimming

the zygote. Binary fission, on the other hand, is an example of *asexual* reproduction.

Notice also another important fact. The spores when first emitted from the ruptured zygote are mere granules of protoplasm, approaching as nearly as anything in nature to the mathematical definition of a point, "without parts and without magnitude." And, during its growth, a spore increases not only in size but also in complexity, in other words undergoes a progressive differentiation or *development.* This is an instance of the principle known as Von Baer's law, according to which "development is a progress from the simple to the complex, from the general to the special, from the homogeneous to the heterogeneous." In Heteromita, then, we have our first instance of development, since in simple fission there is no development, each product of division being, from the first, similar to the parent in all but size.

Lastly, Heteromita is the first instance we have had of an organism with a definite *life-history.* It multiplies asexually by simple fission, producing free-swimming and anchored forms: these conjugate in pairs forming a zygote, in which, by multiple fission, numerous spores are formed: the spores develop into the adult form, asexual multiplication begins once more, and so the cycle of existence is completed.

It must be borne in mind that further researches may reveal the occurrence of a true sexual process in Amœba and Hæmatococcus pluvialis: in other species of Hæmatococcus conjugation of the microzooids is known to take place.

monad which seeks and attaches itself to the anchored form as a male, and the passive anchored form as a female gamete (see Lesson XII.).

LESSON IV

EUGLENA

THE rain-water collected in puddles by the road-side, on roofs, &c., is often found to have a bright green colour: this is sometimes due to the presence of delicate water weeds visible to the naked eye (Lessons XVI. and XIX.), but frequently the water when held up to the light in a glass vessel appears uniformly green, no suspended matter being visible to the unaided sight. Under these circumstances the green colour is frequently due to the presence of vast numbers of an organism known as *Euglena viridis*.

Although microscopic, Euglena is considerably larger than either Hæmatococcus or Heteromita, its length varying from $\frac{1}{24}$ mm. to $\frac{1}{6}$ mm. The body is spindle-shaped, wide in the middle and narrow at both ends (Fig. 5, A—E): one extremity is blunter than the other, and from it proceeds a single long flagellum (*fl*) by the action of which the organism swims with great rapidity, the flagellum being, as in Hæmatococcus, directed forwards. Besides its rapid swimming movements Euglena frequently performs slow movements of contraction and expansion, something like those of a short worm, the body becoming broadened out first at the anterior end, then in the middle, then at the

posterior end, twisting to the right and left, and so on (Fig. 5, A—D). These movements are so characteristic of the genus that the name *euglenoid* is applied to them.

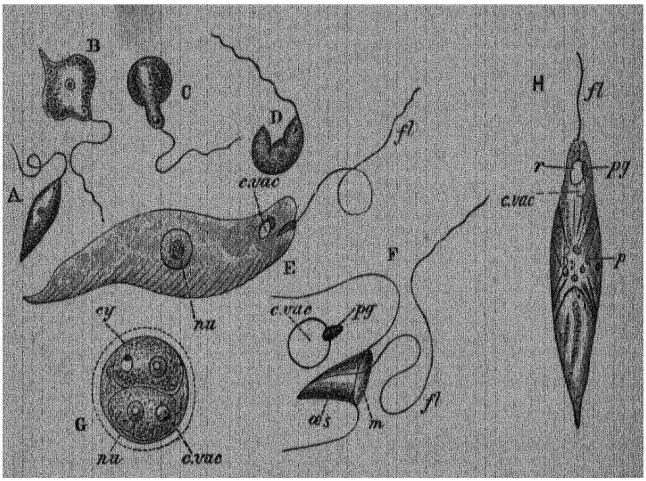

FIG. 5.—*Euglena viridis.*

A—D, four views of the living organism, showing the changes of form produced by the characteristic euglenoid movements.

E, enlarged view, showing the nucleus (*nu*), reservoir of the contactile vacuole (*c. vac*), with adjoining pigment spot, and gullet with a single flagellum springing from it.

F, enlarged view of the anterior end of E, showing pigment-spot (*pg*) and reservoir (*c. vac*), mouth (*m*), gullet (*œs*), and origin of flagellum (*fl*).

G, resting form after binary fission, showing cyst or cell-wall (*cy*), and the nuclei (*nu*) and reservoirs (*c. vac*) of the daughter-cells.

H, active form showing contractile vacuole (*c. vac*), reservoir (*r*), and paramylum-bodies (*p*).

(A—G, after Saville Kent: H, from Bütschli after Klebs.)

The body consists of protoplasm covered with a very delicate skin or *cuticle* which is often finely striated, and is to be looked upon as a superficial hardening of the protoplasm. The green colour is due to the presence of

chlorophyll, which tinges all the central part [redacted] body, the two ends being colourless. It is difficult [redacted] ake out whether the chlorophyll is lodged in one chro[redacted] hore or in several.

In Hæmatococcus we saw that chlorophyll was associated with starch (p. 27). In Euglena there are, near the middle of the body, a number of grains of *paramylum* (H, *p*), a carbohydrate of the same composition as starch ($C_6H_{10}O_5$), but differing from it in remaining uncoloured by iodine.

Water containing Euglena gives off bubbles of oxygen in sunlight: as in Hæmatococcus the carbon dioxide in solution in the water is decomposed in the presence of chlorophyll, its oxygen evolved, and its carbon combined with the elements of water and used in nutrition. For a long time Euglena was thought to be nourished entirely in this way, but there is a good deal of reason for thinking that this is not the case.

When the anterior end of a Euglena is very highly magnified it is found to have the form shown in Fig. 5, F. It is produced into a blunt snout-like extremity at the base of which is a conical depression (*œs*) leading into the soft internal protoplasm:—just the sort of depression one could make in a clay model of Euglena by thrusting one's finger or the end of a pencil into the clay. From the bottom of this tube the flagellum arises, and by its continual movement gives rise to a sort of whirlpool in the neighbourhood. By the current thus produced minute solid food-particles are swept down the tube and forced into the soft internal protoplasm, where they doubtless become digested in the same way as the substances ingested by an Amœba. That solid particles are so ingested by Euglena has been proved by diffusing finely powdered carmine in the water, when the

coloured particles were seen to be swallowed in the way described.

The depression in question is therefore a *gullet*, and its external aperture or margin (*m*) is a *mouth*. Euglena, like Amœba, takes in solid food, but instead of ingesting it at almost any part of the body, it can do so only at one particular point where there is a special ingestive aperture or mouth. This is clearly a case of specialization or differentiation of structure : in virtue of the possession of a mouth and gullet Euglena is more highly organized than Amœba.

It thus appears that in Euglena nutrition is both holozoic and holophytic : very probably it is mainly holophytic during daylight and holozoic in darkness.

Near the centre of the body or somewhat towards the posterior end is a well-marked globular nucleus (E, *nu*), and at the anterior end is a clear space (*c. vac*) looking very like a contractile vacuole. It has been shown, however, that this space is in reality a non-contractile cavity or *reservoir* (H, *r*) into which the true contractile vacuole (*c. vac*) opens, and which itself discharges into the gullet.

In close relation with the reservoir is found a little bright red speck (*pg*) called the *pigment spot* or *stigma*. It consists of hæmatochrome (see p. 26) and is curiously like an eye in appearance, so much so that it is often known as the eye-spot. Recent experiments seem to show that it is specially sensitive to light and is therefore a true eye in the sense of a light-perceiving organ although having no actual visual function.

As in Hæmatococcus a resting condition alternates with the motile phase: the organism loses its flagellum and

surrounds itself with a cyst of cellulose (Fig. 5, G, *cy*), from which, after a period of rest, it emerges to resume active life.

Reproduction takes place by simple fission of the resting form, the plane of division being always longitudinal (G). Sometimes each product of division or daughter-cell divides again: finally the two, or four, or sometimes even eight daughter-cells emerge from the cyst as active Euglenæ. A process of multiple fission (p. 42) has also been described, numerous minute active spores being produced which gradually assume the ordinary form and size.

LESSON V

PROTOMYXA AND THE MYCETOZOA

WHEN Professor Haeckel was investigating the zoology of the Canary Islands more than twenty years ago he discovered a very remarkable organism which he named *Protomyxa aurantiaca*. It was found in sea-water attached to a shell called *Spirula*, and was at once noticeable from the bright orange colour which suggested its specific name. Apparently no one has since been fortunate enough to find it.

In its fully developed stage Protomyxa is the largest of all the organisms we have yet studied, being fully 1 mm. ($\frac{1}{25}$ inch) in diameter, and therefore visible to the naked eye as a small orange speck. In general appearance (Fig. 6, A), it is not unlike an immense Amœba, the chief difference lying in the fact that the pseudopods (*psd*) instead of being short, blunt processes, few in number (comp. Fig. 1, p. 2) are very numerous, slender, branching threads which often unite with one another so as to form networks. No nucleus was observed[1] and no contractile vacuole, but it is quite possible that a renewed examination might prove the presence of one or both of these structures.

The figure (A) is enough to show that nutrition is holozoic;

[1] See p. 9, note.

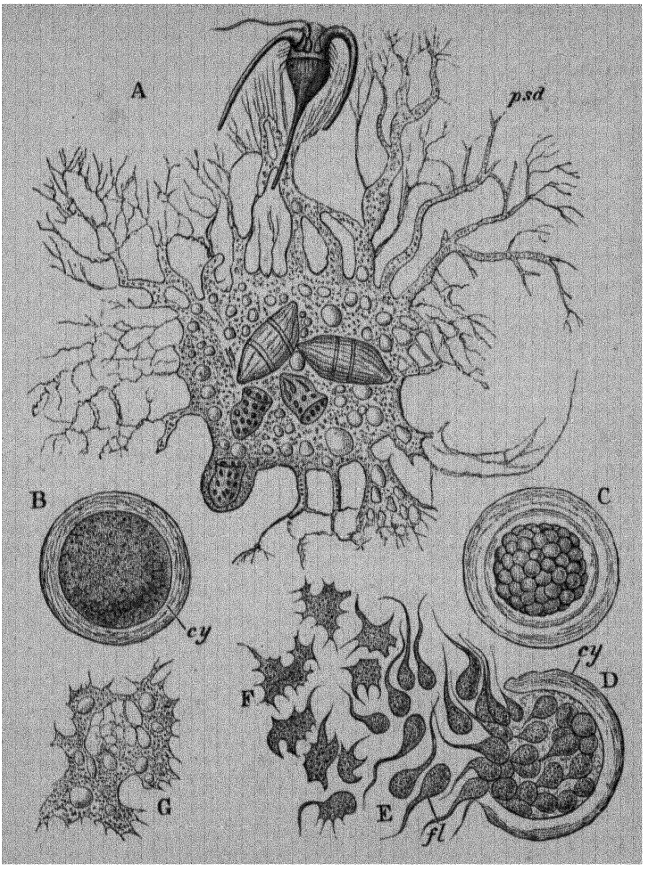

FIG. 6.—*Protomyxa aurantiaca.*

A, the living organism (plasmodium), showing fine branched pseudopods (*psd*) and several ingested organisms.

B, the same, encysted: *cy* the cell-wall

C, the protoplasm of the encysted form breaking up into spores.

D, dehiscence of the cyst and emergence of

F, flagellulæ which afterwards become converted into

E, amœbulæ.

G, amœbulæ uniting to form a plasmodium (After Haeckel.)

the specimen has ingested several minute organisms and is in the act of capturing another.

But the main interest of Protomyxa lies in its very curious and complicated life-history. After crawling over the Spirula shell for a longer or shorter time it draws in its pseudopods, comes to rest, and surrounds itself with a cyst (B, *cy*). The composition of the cyst is not known, but it is apparently not cellulose, since it is not coloured by iodine and sulphuric acid (p. 28).

Next, the encysted protoplasm undergoes multiple fission, dividing into a number of spores (C). Soon the cyst bursts and its contents emerge (D) as bodies which differ utterly in appearance from the amœboid form from which we started. Each spore has in fact become a little ovoid body of an orange colour, provided with a single flagellum (E, *fl*) by the lashing of which it swims through the water after the manner of a monad.

It is convenient to have a name by which to distinguish these flagellate bodies, just as we have special names for the young of the higher animals, such as tadpoles or kittens. From the fact of their distinguishing character being the possession of a flagellum they are called *flagellulæ*; the same name will be applied to the flagellate young of various other organisms which we shall study hereafter.

After swimming about actively for a time each flagellula settles down on some convenient substratum and undergoes a remarkable change: its movements become sluggish, its outline irregular, and its flagellum short and thick, until it finally takes on the form of a little Amœba (F). For this stage also a name is required: it is not an Amœba but an amœboid phase in the life-history of a totally different organism: it is called an *amœbula*.

The process just described may be taken as a practical

proof of the statement made in a previous Lesson (p. 34) that a flagellum is nothing more than a delicate and relatively permanent pseudopod. In Protomyxa we have a flagellula directly converted into an amœbula, the flagellum of the former becoming one of the pseudopods of the latter.

The amœbulæ thus formed may simply increase in size and send out numerous delicate pseudopods, thus becoming converted into the ordinary Protomyxa-form. Frequently, however, they attain this form by a very curious process: they come together in twos and threes until they are in actual contact with one another, when they undergo complete and permanent fusion (G). In this case the Protomyxa-form is produced not by the development of a single amœbula but by the complete fusion of a variable number of amœbulæ. A body formed in this way by the fusion of amœbulæ is called a *plasmodium*, so that in the life-history of Protomyxa we can distinguish an encysted, a ciliated or flagellate, an amœboid, and a plasmodial phase.

The nature of a plasmodium will be made clearer by a brief general consideration of the strange group of organisms known as *Mycetozoa* or sometimes "slime-fungi," to which Protomyxa itself very probably belongs. The best known members of the group occur as gelatinous masses on the bark of trees, on dead leaves, on the surface of tan-pits, and sometimes in water. It must be remembered that *Mycetozoa* is the name not of a genus, but of a *class* in which are included several genera, such as *Badhamia*, *Physarum*, &c. (see Fig. 7): a general account of the class is all that is necessary for our present purpose.

The Mycetozoa consists of sheets or networks of protoplasm which may be as much as 30 cm (1 ft.) in diameter,

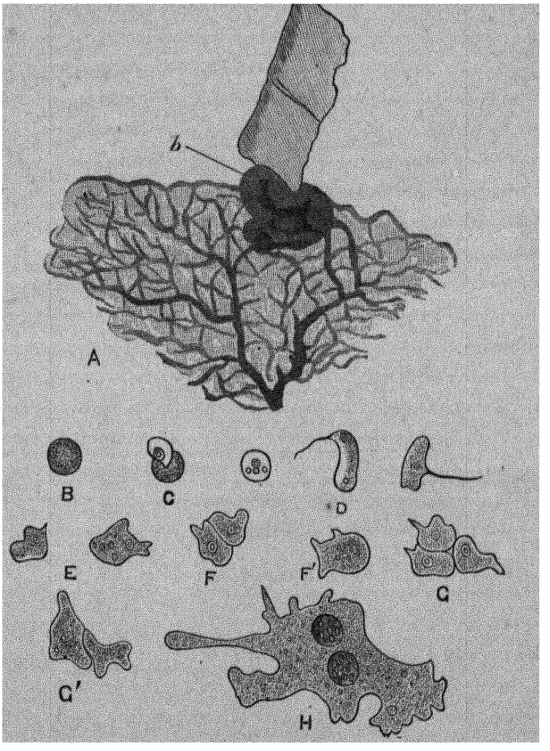

FIG. 7.—A, part of the plasmodium of *Badhamia* (× 3½); *b*, a short pseudopod enclosing a bit of mushroom stem.
B, spore of *Physarum*.
C, the same, undergoing dehiscence.
D, flagellulæ liberated from spores of the same.
E, amœbulæ formed by metamorphosis of flagellulæ.
F, two amœbulæ about to fuse: F', the same after complete union.
G, G', two stages in the formation of a three-celled plasmodium.
H, a small plasmodium.
(A, after Lister: B—H, from Sachs after Cienkowski.)

and throughout the substance of which are found numerous nuclei. In this condition they creep about over bark or some other substance: and in doing so ingest solid food (Fig. 7, A). It has been proved that they digest protoplasm: and in one genus pepsin—the constituent of our own gastric juice by which the digestion of proteids is effected (see p. 12)—has been found. They can also digest starch which has been swollen by a moderate heat—as in our own bread and rice-puddings—but are unable to make use of raw starch.

After living in this free condition, like a gigantic terrestrial Amœba, for a longer or shorter time, either a part or the whole of the protoplasm becomes encysted [1] and breaks up into spores. These (B) consist of a globular mass of protoplasm covered with a wall of cellulose: the cysts are also formed of cellulose.

By the rupture of the cell-wall of the spore (C) the protoplasm is liberated as a flagellula (D) provided with a nucleus and a contractile vacuole, and frequently exhibiting amœboid as well as ciliary movements. After a time the flagellulæ lose their cilia and pass into the condition of amœbulæ (E), which finally fuse to form the plasmodium with which we started (F—H). In the young plasmodia (G^1) the nuclei of the constituent amœbulæ are clearly visible, and from them the nuclei of the fully developed plasmodia are probably derived. It would seem, therefore, that in the fusion of amœbulæ to form the plasmodium of Mycetozoa the cell-bodies (protoplasm) alone coalesce, not the nuclei.

There is a suggestive analogy between this process of

[1] The process of formation of the cyst or sporangium is a complicated one, and will not be described here. See De Bary, *Fungi, Mycetozoa, and Bacteria* (Oxford, 1887), and Lister, *Catalogue of the Mycetozoa* (London, 1894).

plasmodium-formation and that of conjugation as seen in Heteromita. Two Heteromitæ fuse and form a zygote the protoplasm of which divides into spores. In Protomyxa and the Mycetozoa not two but several amœbulæ unite to form a plasmodium which after a time becomes encysted and breaks up into spores. So that we might look upon the conjugation of Heteromita as an extremely simple plasmodial phase in its life-history, or upon the formation of a plasmodium by Protomyxa and the Mycetozoa as a process of multiple conjugation.

There is, however, an important difference between the two cases by reason of which the analogy is far from complete. In Heteromita the nuclei of the two gametes are no longer visible (p. 41) : they coalesce during conjugation, and the product of their union subsequently, in all probability, breaks up to form the nuclei of the spores. In the Mycetozoa neither fusion nor apparent disappearance of the nuclei of the amœbulæ has been observed.

LESSON VI

A COMPARISON OF THE FOREGOING ORGANISMS WITH CERTAIN CONSTITUENT PARTS OF THE HIGHER ANIMALS AND PLANTS

WHEN a drop of the blood of a crayfish, lobster, or crab is examined under a high power, it is found to consist of a nearly colourless fluid, the *plasma*, in which float a number of minute solid bodies, the *blood-corpuscles* or *leucocytes*. Each of these (Fig. 8, A) is a colourless mass of protoplasm, reminding one at once of an Amœba, and on careful watching the resemblance becomes closer still, for the corpuscle is seen to put out and withdraw pseudopods (A^1—A^4) and so gradually to alter its form completely. Moreover the addition of iodine, logwood, or any other suitable colouring matter reveals the presence of a large nucleus (A^5, A^6, *nu*): so that, save for the absence of a contractile vacuole in the leucocyte, the description of Amœba in Lesson I. would apply almost equally well to it.

The blood of a fish, a frog (B^1), a reptile, or a bird contains quite similar leucocytes, but in addition there are found in the blood of these red-blooded animals bodies called *red corpuscles*. They are flat oval discs of protoplasm (B^5, B^6)

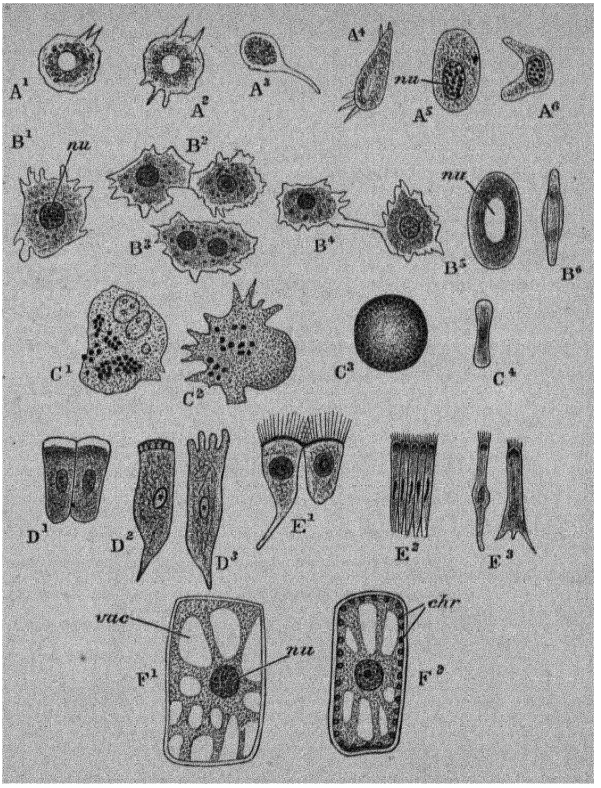

FIG. 8.—Typical Animal and Vegetable Cells.

A[1]—A[4], living leucocyte (blood corpuscle) of a crayfish showing amœboid movements: A[5], A[6], the same, killed and stained, showing the nucleus (*nu*).

B[1], leucocyte of the frog, *nu* the nucleus; B[2], two leucocytes beginning to undergo fusion: B[3], the same after fusion, a binucleate plasmodium being formed: B[4], a leucocyte, undergoing binary fission: B[5], surface view and B[6], edge view of a red corpuscle of the same, *nu*, the nucleus.

C[1], C[2], leucocytes of the newt; in C[1] particles of vermilion, represented by black dots, have been ingested.

C[3], surface view and C[4], edge view of a red corpuscle of man.

D[1], columnar epithelial cells from intestine of frog: D[2], a similar

cell showing striated distal border from which in D³ pseudopods are protruded.

E¹, ciliated epithelial cell from mouth of frog; E², E³, similar cells from windpipe of dog.

F¹, parenchyma cell from root of lily, showing nucleus (*nu*), vacuoles (*vac*), and cell-wall: F², a similar cell from leaf of bean, showing nucleus, vacuoles, cell-wall and chromatophores (*chr*).

(B, D¹, and E¹, after Howes: C, E², and E³, after Klein and Noble Smith: D², D³, after Wiedersheim: F¹, after Sachs: F², after Behrens.)

coloured by a pigment called *hæmoglobin*, and provided each with a large nucleus (*nu*) which, when the corpuscle is seen from the edge (B⁶), produces a bulging of its central part. These bodies may be compared to Amœbæ which have drawn in their pseudopods, assumed a flattened form, and become coloured with hæmoglobin.

In the blood of mammals, such as the rabbit, dog, or man, similar leucocytes occur, but their red blood corpuscles (C³,C⁴) have the form of biconcave discs, and are devoid of nuclei.

In many animals the leucocytes have been observed to ingest solid particles (C¹), to multiply by simple fission (B⁴), and to coalesce with one another forming plasmodia (B², B³) (p. 52).

The stomach and intestines of animals are lined with a sort of soft slimy skin called *mucous membrane*. If a bit of the surface of this membrane—in a frog or rabbit for instance—is snipped off and "teased out," *i.e.*, torn apart with needles, it is found when examined under a high power to be made up of an immense number of microscopic bodies called *epithelial cells*, which in the living animal, lie close to one another in the inner layer of mucous membrane in something the same way as the blocks of a wood pavement lie on the surface of a road. An epithelial cell (D¹, D²) consists of a rod-like mass of protoplasm, containing a large nucleus, and is therefore comparable to an

elongated Amœba without pseudopods. In some animals the resemblance is still closer: the epithelial cells have been observed to throw out pseudopods from their free surfaces (D^3), that is, from the only part where any such movement is possible, since they are elsewhere in close contact with their fellow cells.

The mouth of the frog and the trachea or windpipe of air-breathing vertebrates such as reptiles, birds, and mammals, are also lined with mucous membrane, but the epithelial cells which constitute its inner layer differ in one important respect from those of the stomach and intestine. If examined quite fresh each is found to bear on its free surface, *i.e.*, the surface which bounds the cavity of the mouth or windpipe, a number of delicate protoplasmic threads or *cilia* (E^1—E^3) which are in constant vibratory movement. In the process of teasing out the mucous membrane some of the cells are pretty sure to become detached, and are then seen to swim about in the containing fluid by the action of their cilia. These *ciliated epithelial cells* remind one strongly of Heteromita, except for the fact that they bear numerous cilia in constant rhythmical movement instead of two only—in this case distinguished as flagella—presenting an irregular lashing movement.

Similar ciliated epithelial cells are found on the gills of oysters, mussels, &c., and in many other situations.

The stem or root of an ordinary herbaceous plant, such as a geranium or sweet-pea, is found when cut across to consist of a central mass of pith, around which is a circle of woody substance, and around this again a soft greenish material called the *cortex*. A thin section shows the latter to be made up of innumerable polyhedral bodies called

parenchyma cells, fitting closely to one another like the bricks in a wall.

A parenchyma cell examined in detail (F[1]) is seen to consist of protoplasm hollowed out internally into one or more cavities or *vacuoles* (*vac*) containing a clear fluid. These vacuoles differ from those of Amœba, Heteromita, or Euglena in being non-contractile; they are in fact mere cavities in the protoplasm containing a watery fluid: the layer of protoplasm immediately surrounding them is denser than the rest. Sometimes there is only one such space occupying the whole interior of the cell, sometimes, as in the example figured, there are several, separated from one another by delicate bands or sheets of protoplasm. The cell contains a large nucleus (*nu*) and is enclosed in a moderately thick cell-wall composed of cellulose.

The above description applies to the cells composing the deeper layers of the cortex, *i.e.*, those nearest the woody layer: in the more superficial cells, as well as in the internal cells of a leaf, there is something else to notice. Imbedded in the protoplasm, just within the cell-wall, are a number of minute ovoid bodies of a bright green colour (F[2], *chr*). These are *chromatophores* or chlorophyll corpuscles; they consist of protoplasm coloured with chlorophyll, which can be proved experimentally to have the same properties as the chlorophyll of Hæmatococcus and Euglena.

Such a green parenchyma cell is clearly comparable with an encysted Hæmatococcus or Euglena, the main differences being that in the plant-cell the form is polyhedral owing to the pressure of neighbouring cells and that the chromatophores are relatively small and numerous. Similarly a colourless parenchyma cell resembles an encysted Amœba.

The pith, the epidermis or thin skin which forms the outer surface of herbaceous plants, the greater part of the

leaves, and other portions of the plant may be shown to consist of an aggregation of cells agreeing in essential respects with the above description.

We come therefore to a very remarkable result. The higher animals and plants are built up—in part at least—of elements which resemble in their essential features the minute and lowly organisms studied in previous lessons. Those elements are called by the general name of *cells*: hence the higher organisms, whether plants or animals, are *multicellular* or are to be considered as *cell-aggregates*, while in the case of such beings as Amœba, Hæmatococcus, Heteromita, or Euglena, the entire organism is a single cell, or is *unicellular*.

Note further that the cells of the higher animals and plants, like entire unicellular organisms, may occur in either the amœboid (Fig. 8, A, B^1, C^1,) the ciliated (E), or the encysted (F) condition, and that a plasmodial phase (B^2) is sometimes produced by the union of two or more amœboid cells.

One of the most characteristic features in the unicellular organisms described in the preceding lessons is the constancy of the occurrence of binary fission as a mode of multiplication. The analogy between these organisms and the cells of the higher animals and plants becomes still closer when we find that in the latter also simple fission is the normal mode of multiplication, the increase in size of growing parts being brought about by the continual division of their constituent cells.

The process of division in animal and vegetable cells is frequently accompanied by certain very characteristic and complicated changes in the nucleus to which we must now

direct our attention. First of all, however, it will be necessary to describe the exact microscopic structure of cells and their nuclei as far as it is known at present.

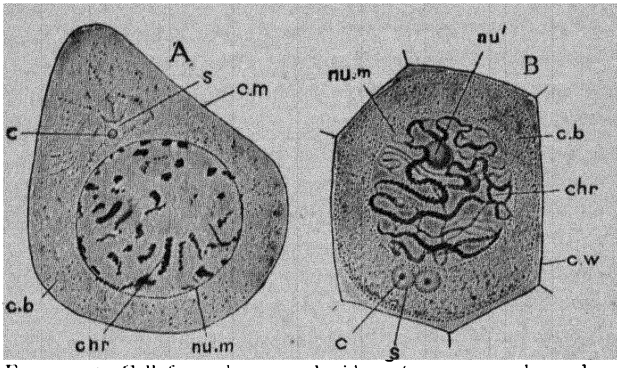

FIG. 9.—A, Cell from the genital ridge of a young salamander, showing cell-membrane (*c. m*), protoplasm or cell-body (*c. b*) with astrosphere (*s*) and centrosome (*c*), and nucleus with membrane (*nu. m*) and irregular network of chromatin (*chr*). B. Cell from the immature stamen of a lily, showing cell-wall (*c. w*), protoplasm, with nucleus as in A. (The astrospheres here figured are incorrect.—*W. N. P.*).

Both figures very highly magnified.

(A, from a drawing by J. E. S. Moore ; B, after Guignard.)

There seems to be a good deal of variation in the precise structure of various animal and plant cells, but the more recent researches show that in the cell-body or protoplasm (Fig. 9, *c. b*) two constituents may be distinguished, a clear semi-fluid substance, traversed by a delicate sponge-work. Now under the microscope the whole cell is not seen at once but only an *optical section* of it, that is all the parts which are in focus at one time : by altering the focus we view the object at successive depths, each view being practically a slice parallel to the lenses of the instrument. This being the case, protoplasm presents the microscopic appearance of a clear or slightly granular

matrix traversed by a delicate network. In the epithelial cells of animals the protoplasm is bounded externally by a *cell-membrane* (Fig. 9, A, *c. m*) of extreme tenuity, in plants by a cell-wall (B, *c. w*) of cellulose: in amœboid cells the ectosarc or transparent non-granular portion of the cell consists of clear protoplasm only, the granular endosarc alone possessing the sponge-work. In the majority of full-grown plant cells (Fig. 8, F) and in some animal cells the protoplasm is more or less extensively vacuolated, but in the young growing parts as well as in the ordinary cells of animals the foregoing description holds good. It is quite possible that the reticular character of the protoplasm may be merely the optical expression of an extensive but minute vacuolation, or may be due to the presence of innumerable minute granules developed in the protoplasm as products of metabolism.

The nucleus is usually spherical in form: it is enclosed in a delicate *nuclear membrane* (*nu.m*) and contains, as in Amœba (p. 7) two constituents, the *nuclear sap* and the *chromatin* which exhibit far more striking differences than the two constituents of the cell-body. The nuclear sap is a homogeneous semi-fluid substance which forms the ground-work of the nucleus: it resembles the clear cell-protoplasm in its general characters, amongst other things in being unaffected by dyes. The chromatin (*chr*) takes the form of a network or sponge-work of very variable form, and is distinguished from all other constituents of the cell by its strong affinity for aniline and other dyes. Frequently one or more minute globular structures, the *nucleoli* (B, *nu'*), occur in the nucleus either connected with the network or lying freely in its meshes: they also have a strong affinity for dyes although they often differ considerably from the chromatin in their micro-chemical reactions.

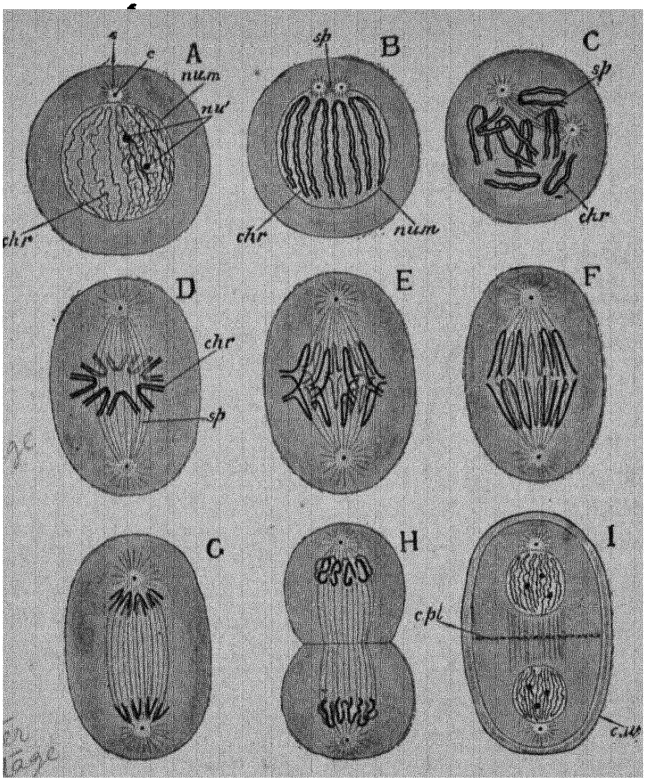

FIG. 10.—Diagrams illustrating the process of indirect cell division or mitosis.

A, the resting cell: the nucleus shows a nuclear membrane (*nu. m*), chromatin (*chr*) arranged in loops united into a network (the latter shown on the right side only), and two nucleoli (*nu'*): near the nucleus is an astrosphere (*s*), containing a centrosome (*c*) and surrounded by radiating protoplasmic filaments.

B, The chromatin has resolved itself into distinct loops or chromosomes (*chr*) which have divided longitudinally: the nuclear membrane has begun to disappear: there are two astrospheres and between them is seen the commencement of the nuclear spindle (*sp*).

C, The nuclear membrane has disappeared: the chromosomes are

arranged irregularly: the spindle has increased in size and is situated definitely within the nuclear area.

D, The chromosomes are arranged round the equator of the fully formed nuclear spindle.

E, The daughter-loops of the chromosomes are passing in opposite directions towards the poles of the spindle, each having a spindle-fibre attached to it.

F, Later stage of the same process.

G, The chromosomes are now arranged in two distinct groups, one at each pole of the spindle.

H, The daughter-cells are partly separated by constriction and the chromosomes of each group are uniting to form the network of the daughter-nucleus.

I, Shows the division of a plant cell by the formation of a cell-plate (*c. pl*): the daughter nuclei are fully formed.

(Altered from Flemming, Rabl, &c.)

In the body of some cells and possibly of all there is found a globular body, surrounded by a radiating arrangement of the protoplasm and called the *astrosphere* (*s*): it lies close to the nucleus, and contains a minute granule known as the *central particle* or *centrosome* (*c*). In many cells two astrospheres and two or more centrosomes have been found in each cell (B, *s*).

The precise changes which take place during the fission of a cell are, like the structure of the cell itself, subject to considerable variation. We will consider what may probably be taken as a typical case (Fig. 10).

First of all, the astrosphere, with its centrosome, divides (B) and the products of its division gradually separate from one another (C), ultimately passing to opposite poles of the nucleus (D). At the same time the network of chromatin divides into a number of separate filaments called *chromosomes* (B, *chr*), the number of which appears to be constant in any given species of animal or plant, although it may vary in different species from 2 to 168 or more. Soon after this the nuclear membrane and the free nucleoli disappear (B, C) and the

nucleus is seen to contain a spindle shaped body (*sp*) formed of excessively delicate fibres which converge at each pole to the corresponding astrosphere. The precise origin of this nuclear spindle is uncertain: it may arise either from the nuclear matrix or, more probably, from the protoplasm of the cell: it is not affected by colouring matters.

At the same time each chromosome splits along its whole length so as to form two parallel rods or loops in close contact with one another (B): in this way the number of chromosomes is doubled, each one being now represented by a couple.

The divided chromosomes now pass to the equator of the spindle (D) and assume the form of more or less V-shaped loops, which arrange themselves in a radiating manner so as to present a star-like figure when the cell is viewed in the direction of the long axis of the spindle. Everything is now ready for division to which all the foregoing processes are preparatory.

The two chromosomes of each couple now gradually pass to opposite poles of the spindle (E, F), two distinct groups being thus produced (G) and each chromosome of each group being the twin of one in the other group. Perhaps the fibres of the spindle are the active agents in this process, the chromosomes being dragged in opposite directions by their contraction: on the other hand it is possible that the movement is due to the contractility of the chromosomes themselves.

After reaching the poles of the spindle the chromosomes of each group unite with one another to form a network (H) around which a nuclear membrane finally makes its appearance (I). In this way two nuclei are produced within a single cell, the chromosomes of the *daughter-nuclei*, as well

as their attendant astrospheres, being formed by the binary fission of those of the *mother-nucleus*.

But *pari passu* with the process of nuclear division, fission of the cell-body is also going on. This may take place by a simple process of constriction (II) –in much the same way as a lump of clay or dough would divide if a loop of string were tied round its middle and then tightened –or by the formation of what is known as a *cell-plate*. This arises as a row of granules formed from the equatorial part of the nuclear spindle (I): the granules extend until they form a complete equatorial plate dividing the cell-body into two halves: fission then takes place by the cell-plate splitting into two along a plane parallel with its flat surfaces.[1] In plants the cell-plate gives rise to a partition wall of cellulose which divides the two daughter-cells from one another.

In some cases the dividing nucleus, instead of going through the complicated processes just described, divides by simple constriction. We have therefore to distinguish between *direct* and *indirect nuclear division*. To the latter very elaborate method the name *mitosis* or *karyokinesis* is applied: direct division is then distinguished as *amitotic*.

In this connection the reader will not fail to note the extreme complexity of structure revealed in cells and their nuclei by the highest powers of the microscope. When the constituent cells of the higher animals and plants were discovered, during the early years of the present century, by Schleiden and Schwann, they were looked upon as the *ultima Thule* of microscopic analysis. Now the demonstration of

[1] It must not be forgotten that the cells, which are necessarily represented in such diagrams as Fig. 10 as planes, are really solid bodies, and that consequently the cell-plate represented in the figures as a line is actually a plane at right angles to the plane of the paper.

the cells themselves is an easy matter, the problem is to make out their ultimate constitution. What would be the result if we could get microscopes as superior to those of to-day as those of to-day are to the primitive instruments of eighty or ninety years ago, it is impossible even to conjecture. But of one thing we may feel confident—of the enormous strides which our knowledge of the constitution of living things is destined to make during the next half century.

The striking general resemblance between the cells of the higher animals and plants and entire unicellular organisms has been commented on as a very remarkable fact: there is another equally significant circumstance to which we must now advert.

All the higher animals begin life as an egg, which is either passed out of the body of the parent as such, as in most fishes, frogs, birds, &c., or undergoes the first stages of its development within the body of the parent, as in sharks, some reptiles, and nearly all mammals.

The structure of the egg is, in essential respects, the same in all animals from the highest to the lowest. In a jelly-fish, for instance, it consists (Fig. 11, A) of a globular mass of protoplasm (*gd*), in which are deposited granules of a proteinaceous substance known as *yolk-spherules*. Within the protoplasm is a large clear nucleus (*g.v*) the chromatin of which is aggregated into a central mass or nucleolus (*g.m*). An investing membrane may or may not be present. In other words the egg is a cell: it is convenient, for reasons which will appear immediately, to speak of it as the *ovum* or *egg-cell*.

The young or immature ova of all animals present this structure, but in many cases certain modifications are undergone before the egg is mature, *i.e.*, capable of development

into a new individual. For instance, the protoplasm may throw out pseudopods, the egg becoming amœboid (see Fig. 52); or the surface of the protoplasm may secrete a thick cell-wall (see Fig. 61). The most extraordinary modification takes place in some Vertebrata, such as birds. In a hen's egg, for instance, the yolk-spherules increase immensely, swelling out the microscopic ovum until it becomes what we know as the "yolk" of the egg: around this layers of albumen or "white" are deposited, and finally the shell membrane and the shell. Hence we have to distinguish carefully in eggs of this character between the entire "egg" in the ordinary acceptation of the term, and the ovum or egg-cell.

But complexities of this sort do not alter the fundamental

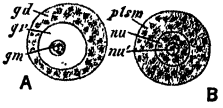

FIG. 11.—A, ovum of an animal (*Carmarina hastata*, one of the jelly fishes), showing protoplasm (*gd*), nucleus (*gv*), and nucleolus (*gm*). B, ovum of a plant (*Gymnadenia conopsea*, one of the orchids), showing protoplasm (*plsm*), nucleus (*nu*), and nucleolus (*nu'*).
(A, from Balfour after Haeckel: B, after Marshall Ward.)

fact that all the higher animals begin life as a single cell, or in other words that multicellular animals, however large and complex they may be in their adult condition, originate as unicellular bodies of microscopic size.

The same is the case with all the higher plants. The pistil or seed-vessel of an ordinary flower contains one or more little ovoidal bodies, the so-called "ovules" (more accurately megasporangia—see Lesson XXXIV., and Fig. 127), which, when the flower withers, develop into the seeds. A

section of an ovule shows it to contain a large cavity, the embryo-sac or megaspore (see Fig. 126, D), at one end of which is a microscopic cell (*or*, and Fig. 11 B), consisting as usual of protoplasm (*plsm*), nucleus (*nu*). and nucleolus (*nu'*). This is the ovum or egg-cell of the plant: from it the new plant, which springs from the germinating seed, arises. Thus the higher plants, like the higher animals, are, in their earliest stages of existence, microscopic and unicellular.

especially in the case of animal infusions, quickly becomes very strong and disagreeable.

The scum after attaining a perceptible thickness breaks up and falls to the bottom, and after this the fluid slowly clears again, becoming once more quite transparent and losing its bad smell. If exposed to the light, patches of green appear in it sooner or later, due to the presence of microscopic organisms containing chlorophyll. The fluid has acquired, in fact, the characteristics of an ordinary stagnant pond, and is quite incapable of further putrefaction. The whole series of changes may occupy many months.

Microscopic examination shows that the freshly-prepared fluid is free from organisms, and indeed, if properly filtered,

FIG. 13 —*Bacterium termo.* A, motile stage : B, resting stage, or zoogloea. (From Klein.)

from particles of any sort. But the case is very different when a drop of infusion in which turbidity has set in is placed under a high power. The fluid is then seen to be crowded with incalculable millions of minute specks, only just visible under a power of 300 or 400 diameters, and all in active movement. These specks are *Bacteria*, or as they are sometimes called, *microbes* or *micro-organisms ;* they belong to the particular genus and species called *Bacterium termo.*

Seen under the high power of an ordinary student's microscope Bacterium termo has the appearance shown in Fig. 13, A : it is like a minute finger-biscuit, *i.e.* has the form

of a rod constricted in the middle. But it is only by using the very highest powers of the microscope that its precise form and structure can be satisfactorily made out. It is then seen (Fig. 14) to consist of a little double spindle, staining very deeply with aniline dyes. By the employment of very high powers it has been shown that the protoplasm of the cell contains a nucleus and is covered with a membrane of extreme tenuity formed either of cellulose or of a proteid material. According to Dallinger, at each end is attached a flagellum about as long as the cell itself.

Bacterium termo is much smaller that any organism we have yet considered, so small in fact that, as it is always easier to deal with whole numbers than with fractions, its

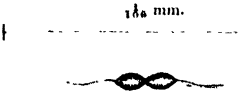

FIG. 14.—*Bacterium termo* (× 4000), showing the terminal flagella. (After Dallinger.)

size is best expressed by taking as a standard the one-thousandth of a millimetre, called a *micromillimetre* and expressed by the symbol μ. The entire length of the organism under consideration is from 1·5 to 2 μ, *i.e.* about the $\frac{1}{500}$ mm. or the $\frac{1}{12500}$ inch. In other words, its entire length is not more than one-fourth the diameter of a yeast-cell or of a human blood-corpuscle. The diameter of the flagellum has been estimated by Dallinger to be about $\frac{1}{8}$ μ or $\frac{1}{20400}$ inch, a smallness of which it is as difficult to form any clear conception as of the distances of the fixed stars.

Some slight notion of these almost infinitely small dimensions may, however, be obtained in the following way. Fig. 14 shows a Bacterium termo magnified 4000 diameters, the

scale above the figure representing $\frac{1}{100}$ mm. magnified to the same amount. The height of this book is a little over 18 cm.; this multiplied by 4,000 gives 72,000 cm. = 720 metres = 2362 feet. We therefore get the proportion—*as* 2362 feet, or nearly six times the height of St. Paul's, *is to* the height of the present volume, *so* the length of Fig. 14 *is to* that of Bacterium termo.

It was mentioned above that at a certain stage of putrefaction a scum forms on the surface of the fluid. This film consists of innumerable motionless Bacteria imbedded in a transparent gelatinous substance formed of a proteid material (Fig. 13, B). After continuing in the active condition for a time the Bacteria rise to the surface, lose their flagella, and throw out this gelatinous substance in which they lie imbedded. The bacterial jelly thus formed is called a *zoogloea*. Thus in Bacterium termo, as in so many of the organisms we have studied, there is an alternation of an active with a resting condition.

During the earlier stages of putrefaction Bacterium termo is usually the only organism found in the fluid, but later on other microbes make their appearance. Of these the commonest are distinguished by the generic names *Micrococcus*, *Bacillus*, *Vibrio*, and *Spirillum*.

Micrococcus (Fig. 15) is a minute form, the cells of which are about 2μ ($\frac{1}{5000}$ mm.) in diameter. It differs from Bacterium in being globular instead of spindle-shaped and in having no motile phase. Like Bacterium it assumes the zooglæa condition (Fig. 15, 4).

Bacillus is commonly found in putrescent infusions in which the process of decay has gone on for some days: as its numbers increase those of Bacterium termo diminish.

until Bacillus becomes the dominant form. Its cells (Fig. 16) are rod shaped and about 6μ ($\frac{1}{1700}$ mm.) in length in the commonest species. Both motionless and active forms are found, the latter having a flagellum at each end. The zooglæa condition is often assumed, and the rods are frequently found united end to end so as to form filaments.

Vibrio resembles Bacillus, but the rod-like cells (Fig. 17, A) are wavy instead of straight. They are actively motile and when highly magnified are found to be provided with a

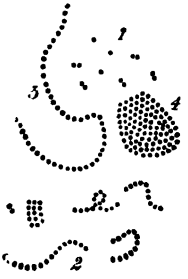

FIG. 15. *Micrococcus*. 1, single and double (dumb-bell shaped) forms: 2 and 3, chain-forms: 4, a zooglæa.

flagellum at each end. Vibriones vary from 8μ to 25μ in length.

Spirillum is at once distinguished by its spiral form, the cells resembling minute corkscrews (Fig. 17, B & C) and being provided with a flagellum at each end (C). The smaller species, such as S. tenue (B) are from 2 to 5 μ in length, but the larger forms, such as S. volutans (C) attain a length of from 25 to 30μ. In swimming Spirillum appears on a superficial examination to undulate like a worm or a serpent, but this is an optical illusion; the spiral is really a permanent one, but during progression it rotates upon its

long axis, like Hæmatococcus (p. 25), and this double movement produces the appearance of undulation.

Most Bacteria are colourless, but three species (*Bacterium viride*, *B. chlorinum*, and *Bacillus virens*) contain chlorophyll, and several others form pigments of varying tints and often of great intensity. For instance, there are red, yellow, brown, blue, and violet species of Micrococcus which grow

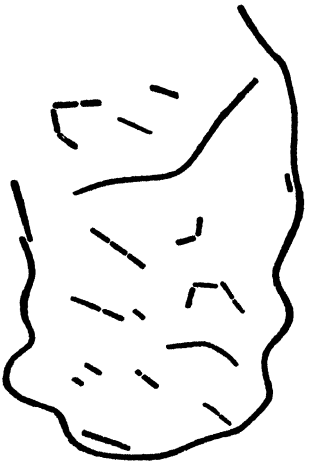

FIG. 16.—*Bacillus subtilis*, showing various stages between single forms and long filaments (*Leptothrix*).

on slices of boiled potato, hard-boiled egg, &c., forming brilliantly coloured patches; and the yellow colour often assumed by milk after it has been allowed to stand for a considerable time is due to the presence of *Bacterium xanthinum*.

All Bacteria multiply by simple transverse fission, the process taking place sometimes during the motile, sometimes during the resting condition. Frequently the daughter-cells do not separate completely from one another but remain

loosely attached, forming chains. This is very common in some species of Micrococcus (See Fig. 15).

Bacillus when undergoing fission behaves something like Heteromita: the mother cell divides transversely across the middle, and the two halves gradually wriggle away from one another, but remain connected for a time by a very fine thread

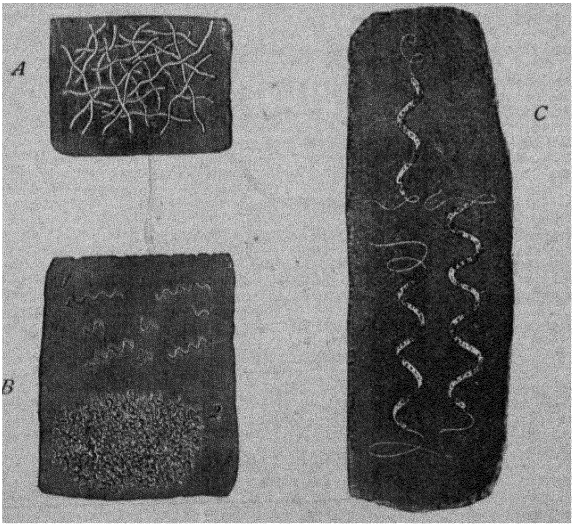

FIG. 17.—A, *Vibrio*. B, *Spirillum tenue*. C, *Spirillum volutans*. (From Klein.)

of protoplasm which extends between their adjacent ends. This is drawn out by the gradual separation of the two cells, until it attains twice the length of a flagellum, when it snaps in the middle, thus providing each daughter-cell with a new flagellum. Bacillus may, however, divide while in the motile condition and, under certain circumstances, the process is repeated again and again, and the daughter-cells,

remaining in contact, form a long wavy or twisted filament called *Leptothrix* (Fig. 16) the separate elements of which are usually only visible after staining.

Bacillus also multiplies by a peculiar process of spore-formation which may take place either in the ordinary resting form or in a Leptothrix filament. A bright dot appears at one place in the protoplasm (Fig. 18): this increases in size, the greater part of the protoplasm being used up in its formation, and finally takes on the form of a clear oval spore which remains for some time enclosed in the cell wall of the Bacillus, by the rupture of which it is finally liberated. In other Bacteria spores are formed directly from the ordinary cells which become thick walled. The spores differ from the Bacilli in being unstained by aniline dyes.

After a period of rest the spores, under favourable circumstances, germinate by growing out at one end so as to become rod-like, and thus finally assuming the form of ordinary Bacilli.

There are other genera often included among Bacteria, for the description of which the student is referred to the more special treatises.[1] One remark must, however, be made in concluding the present brief account of the morphology of the group. There is a great deal of evidence to show that what have been spoken of as genera (Bacterium, Bacillus, Spirillum, &c.) may merge into one another and are therefore to be looked upon as phases in the life-history of various microbes rather than as true and distinct genera. But this is a point which cannot at present be considered as settled.

The conditions of life of Bacteria are very various. Some live in water, such as that of stagnant ponds, and of these

[1] See especially De Bary, *Fungi, Mycetozoa, and Bacteria* (Oxford, 1887), and Klein, *Micro-organisms and Disease* (London, 1896).

three species, as already stated (p. 87), contain chlorophyll. The nutrition of such forms must obviously be holophytic, and in the case of Bacterium chlorinum the giving off of oxygen in sunlight has actually been proved.

But this mode of nutrition is rare among the Bacteria: nearly all of those to which reference has been made are

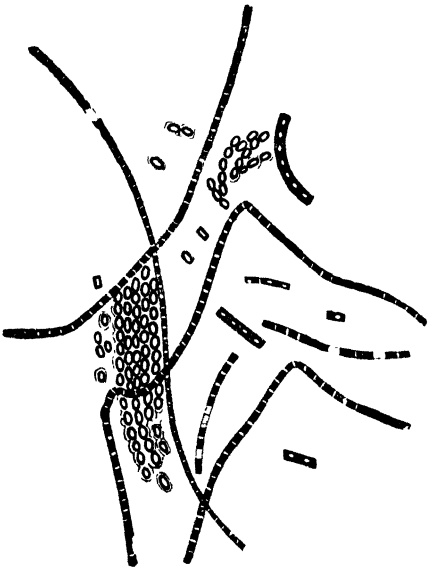

FIG. 18.—Spore-formation in *Bacillus*. (From Klein.)

saprophytes, that is, live upon decomposing animal and vegetable matters. They are, in fact, nourished in precisely the same way as Heteromita (see p. 37). Many of these forms, such as Bacterium termo and species of Bacillus, Vibrio, &c., will, however, flourish in Pasteur's solution, in which they obtain their nitrogen in the form of ammonium

tartrate instead of decomposing proteid. It has also been shown that some Bacteria can go further and make use of nitrates as a source of nitrogen, and of a carbonate or even of carbon dioxide as a source of carbon: in other words, they are able to live upon purely inorganic matter in spite of the fact that they contain no chlorophyll. Some species may even multiply to a considerable extent in distilled water.

But *pari passu* with their ordinary nutritive processes, many Bacteria exert an action on the fluids on which they live comparably to that exerted on a saccharine solution by the yeast-plant. Such microbes are, in fact, organized ferments (see p. 81).

Every one is familiar with the turning sour of milk. This change is due to the conversion of the milk-sugar into lactic acid.

$$\underset{\text{Sugar.}}{C_6H_{12}O_6} = 2\underset{\text{Lactic Acid.}}{(C_3H_6O_3)},$$

The transformation is brought about by the agency of *Bacterium lactis*, a microbe closely resembling *B. termo*.

Beer and wine are two other fluids which frequently turn sour, there being in this case a conversion of alcohol into acetic acid, represented by the equation—

$$\underset{\text{Alcohol.}}{C_2H_6O} + \underset{\text{Oxygen.}}{O_2} = \underset{\text{Water.}}{H_2O} + \underset{\text{Acetic Acid.}}{C_2H_4O_2},$$

The ferment in this instance is *Bacterium aceti*, often called *Mycoderma aceti*, or the "vinegar plant." It will be noticed that in this case oxygen enters into the reaction: it is a case of fermentation by oxidation.

Putrefaction itself is another instance of fermentation induced by a microbe. Bacterium termo—the putrefactive ferment—causes the decomposition of proteids into simpler compounds, amongst which are such gases as ammonia

(NH_3), sulphuretted hydrogen (H_2S), and ammonium sulphide ($(NH_4)_2S$), the evolution of which produces the characteristic odour of putrefaction.

The final stage in putrefaction is the formation of nitrates and nitrites. The process is a double one, both stages being due to special forms of Bacteria. In the first place, by the agency of the *nitrous ferment*, ammonia is converted into nitrous acid—

$$NH_3 + 3O = H_2O + HNO_2$$

Ammonia. Oxygen. Water. Nitrous Acid.

The *nitric ferment* then comes into action, converting the nitrous into nitric acid—

$$NHO_2 + O = HNO_3$$

Nitrous Acid. Oxygen. Nitric Acid.

This process is one of vast importance, since by its agency the soil is constantly receiving fresh supplies of nitric acid which is one of the most important substances used as food by plants.

Besides holophytes and saprophytes there are included among Bacteria many *parasites*, that is, species which feed not on decomposing but on living organisms. Many of the most deadly infectious diseases, such as tuberculosis, diphtheria, typhoid fever, and cholera, are due to the presence in the tissues or fluids of the body of particular species of microbes, which feed upon the parts affected and give rise to the morbid symptoms characteristic of the disease.

Some Bacteria, like the majority of the organisms previously studied, require free oxygen for their existence, but others, like Saccharomyces during active fermentation (see p. 80), are quite independent of free oxygen and must therefore be able to take the oxygen, without which their metabolic

processes could not go on, from some of the compounds contained in the fluid in which they live. Bacteria are for this reason divided into *aerobic* species which require free oxygen, and *anaerobic* species which do not.

As to temperature, common observation tells us that Bacteria flourish only within certain limits. We know for instance that organic substances can be preserved from putrefaction by being kept either at the freezing-point, or at or near the boiling-point. One important branch of modern industry, the trade in frozen meat, depends upon the fact that the putrefactive Bacteria, like other organisms, are rendered inactive by freezing, and every housekeeper knows how easily putrefaction can be staved off by roasting or boiling. Similarly it is a matter of common observation that a moderately high temperature is advantageous to these organisms, the heat of summer or of the tropics being notoriously favourable to putrefaction. In the case of Bacterium termo, it has been found that the optimum temperature is from 30° to 35° C., but that the microbe will flourish between 5° and 40° C.

Although fully-formed Bacteria, like other organisms, are usually killed by exposure to heat several degrees below boiling-point, yet the spores of some species will withstand, at any rate for a limited time, a much higher temperature—even one as high as 130° C. On the other hand, putrefactive Bacteria retain their power of development after being exposed to a temperature of −111° C., although during the time of exposure all vital activity is of course suspended.

Bacteria also resemble other organisms in being unable to carry on active life without a due supply of water: no perfectly dry substance ever putrefies. The preservation for ages of the dried bodies of animals in such countries as Egypt and Peru depends at least as much upon the moistureless air as upon the antiseptics used in embalming.

For the most part Bacteria are unaffected by light, since they grow equally well in darkness and in ordinary daylight. Many of them, however, will not bear prolonged exposure to direct sunlight, and it has been found possible to arrest the putrefaction of an organic infusion by *insolation*, or exposure to the direct action of the sun's rays. It has also been proved that it is the light rays and not the heat-rays which are thus prejudicial to the life of micro organisms.

LESSON IX

BIOGENESIS AND ABIOGENESIS: HOMOGENESIS AND HETEROGENESIS

THE study of the foregoing living things and especially of Bacteria, the smallest and probably the simplest of all known organisms, naturally leads us to the consideration of one of the most important problems of biology—the problem of the origin of life.

In all the higher organisms we know that each individual arises in some way or other from a pre-existing individual: no one doubts that every bird now living arose by a process of development from an egg formed in the body of a parent bird, and that every tree now growing took its origin either from a seed or from a bud produced by a parent plant. But there have always—until quite recently, at any rate—been upholders of the view that the lower forms of life, bacteria, monads, and the like, may under certain circumstances originate independently of pre-existing organisms: that, for instance, in a flask of hay-infusion or mutton broth, boiled so as to kill any living things present in it, fresh forms of life may arise *de novo*, may in fact be created then and there.

We have therefore two theories of the origin of the lower

organisms, the theory of *Biogenesis*, according to which each living thing, however simple, arises by a natural process of budding, fission, spore-formation, or what not, from a parent organism: and the theory of *Abiogenesis*, or as it is sometimes called *Spontaneous* or *Equivocal Generation*, according to which fully formed living organisms sometimes arise from not-living matter.

In former times the occurrence of abiogenesis was universally believed in. The expression that a piece of meat has "bred maggots"; the opinion that parasites such as the gall-insects of plants or the tape-worms in the intestines of animals originate where they are found; the belief still held in some rural districts in the occurrence of showers of frogs, or in the transformation of horse-hairs kept in water into eels; all indicate a survival of this belief.

Aristotle, one of the greatest men of science of antiquity, explicitly teaches abiogenesis. He states that some animals "spring from putrid matter," that certain insects "spring from the dew which falls upon plants," that thread-worms "originate in the mud of wells and running waters," that fleas "originate in very small portions of corrupted matter," and that "bugs proceed from the moisture which collects on the bodies of animals, lice from the flesh of other creatures."

Little more than 200 years ago one Alexander Ross, commenting on Sir Thomas Browne's doubt as to "whether mice may be bred by putrefaction," says, "so may he doubt whether in cheese and timber worms are generated; or if beetles and wasps in cow's dung; or if butterflies, locusts, grasshoppers, shell-fish, snails, eels, and such like, be procreated of putrefied matter, which is apt to receive the form of that creature to which it is by formative power disposed. To question this is to question reason, sense, and experience.

If he doubts of this let him go to Egypt, and there he will find the fields swarming with mice, begot of the mud of Nylus, to the great calamity of the inhabitants."

As accurate inquiries into these matters were made, the number of cases in which equivocal generation was supposed to occur was rapidly diminished. It was a simple matter when once thought of—to prove, as Redi did in 1638, that no maggots were ever "bred" in meat on which flies were prevented by wire screens from laying their eggs. Far more difficult was the task, also begun in the seventeenth century, of proving that parasites, such as tape-worms, arise from eggs taken in with the food; but gradually this proposition was firmly established, so that no one of any scientific culture continued to believe in the abiogenetic origin of the more highly organized animals any more than in showers of frogs, or in the origin of geese from barnacles.

But a new phase of the question was opened with the invention of the microscope. In 1683, Anthony van Leeuwenhoek discovered Bacteria, and it was soon found that however carefully meat might be protected by screens, or infusions by being placed in well-corked or stoppered bottles, putrefaction always set in sooner or later, and was invariably accompanied by the development of myriads of bacteria, monads, and other low organisms. It was not surprising, considering the rapidity with which these were found to make their appearance, that many men of science imagined them to be produced abiogenetically.

Let us consider exactly what this implies. Suppose we have a vessel of hay-infusion, and in it a single Bacterium. The microbe will absorb the nutrient fluid and convert it into fresh protoplasm: it will divide repeatedly, and, its progeny repeating the process, the vessel will soon con-

tain millions of Bacteria instead of one. This means, of course, that a certain amount of fresh living protoplasm has been formed out of the constituents of the hay-infusion, through the agency, in the first instance, of a single living Bacterium. The question naturally arises, Why may not the formation of protoplasm take place independently of this insignificant speck of living matter?

It must not be thought that this question is in any way a vain or absurd one. That living protoplasm has at some period of the world's history originated from not-living matter seems a necessary corollary of the doctrine of evolution, and is obviously the very essence of the doctrine of special creation; and there is no *a priori* reason why it should be impossible to imitate the unknown conditions under which the process took place. At present, however, we have absolutely no data towards the solution of this fundamental problem.

But however insoluble may be the question as to how life first dawned upon our planet, the origin of living things at the present day is capable of investigation in the ordinary way of observation and experiment. The problem may be stated as follows:—Any putrescible infusion—*i.e.* any fluid capable of putrefaction—will be found after a longer or shorter exposure to swarm with bacteria and monads: do these organisms, or the spores from which they first arise, reach the infusion from without, or are they generated within it? And the general lines upon which an investigation into the problem must be conducted are simple: given a vessel of any putrescible infusion; let this be subjected to some process which, without rendering it incapable of supporting life, shall kill any living things contained in it; and let it then be placed under such circumstances that no living particles, however small, can reach it from without. If,

after these two conditions have been rigorously complied with, living organisms appear in the fluid, such organisms must have originated abiogenetically.

To kill any microbes contained in the fluid it is usually quite sufficient to boil it thoroughly. As we have seen, protoplasm enters into heat-rigor at a temperature considerably below the boiling-point of water, so that, with an exception which will be referred to presently, a few minutes' boiling suffices to *sterilize* all ordinary infusions, *i.e.*, to kill any organisms they may contain.

Then as to preventing the entrance of organisms or their spores from without. This may be done in various ways. One way is to take a flask with the neck drawn out into a very slender tube, to boil the fluid in it for a sufficient time, and then, while ebullition is going on, to close the end of the tube by melting the glass in the flame of a Bunsen-burner or spirit-lamp, thus hermetically sealing the flask.

By this method not only organisms and their spores are excluded from the flask but also air. But this is obviously unnecessary: it is evident that air may be admitted to the fluid with perfect impunity if only it can be filtered, that is, passed through some substance which shall retain all solid particles however small, and therefore of course bacteria, monads, and their spores.

A perfectly efficient filter for this purpose is furnished by cotton-wool. A flask or test-tube is partly filled with the infusion: the latter is boiled, and during ebullition cotton-wool is pushed into the mouth of the vessel until a long and firm plug is formed (Fig. 19). When the source of heat is removed, and, by the cooling of the fluid, the steam which filled the upper part of the tube condenses, air passes in to supply its place, but as it does so it is filtered of even the

smallest solid particles by having to pass through the close meshes of the cotton-wool.

Experiments of this sort conducted with proper care have been known for many years to give negative results in the great majority of cases : the fluids remain perfectly sterile for any length of time. But in certain instances, in spite of the most careful precautions, bacteria were found to appear

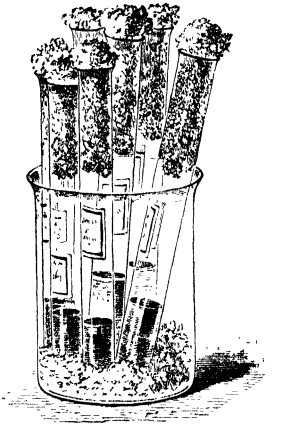

FIG. 19.—A Beaker with a number of test-tubes containing putrescible infusions and plugged with cotton-wool. (From Klein.)

in such fluids; and for years a fierce controversy raged between the biogenists and the abiogenists, the latter insisting that the experiments in question proved the occurrence of spontaneous generation, while the biogenists considered that all such cases were due to defective methods—either to imperfect sterilization of the fluid or to imperfect exclusion of germ-containing atmospheric dust.

The matter was finally set at rest, and the biogenists

proved to be in the right, by the important discovery that the spores of bacteria and monads are not killed by a temperature many degrees higher than is sufficient to destroy the adult forms: that in fact while the fully developed organisms are killed by a few minutes' exposure to a temperature of 70° C. the spores are frequently able to survive several hours' boiling, and must be heated to 130°—150° C. in order that their destruction may be assured. It was also, shown that the more thoroughly the spores are dried the more difficult they are to kill, just as well-dried peas are hardly affected by an amount of boiling sufficient to reduce fresh ones to a pulp.

This discovery of the high thermal death-point or ultra-maximum temperature of the spores of these organisms has necessitated certain additional precautions in experiments with putrescible infusions. In the first place the flask and the cotton-wool should both be heated in an oven to a temperature of 150° C., and thus effectually sterilized. The flask being filled and plugged with cotton-wool is well boiled, and is then kept for some hours at a temperature of 32°—38° C., the optimum temperature for bacteria. The object of this is to allow any spores which have not been killed by boiling to germinate, in other words to pass into the adult condition in which the temperature of boiling water is fatal. The infusion is then boiled again, so as to destroy any such freshly germinated forms it may contain. The same process is repeated once or twice, the final result being that the very driest and most indurated spores are induced to germinate, and are thereupon slain. It must not be forgotten that repeated boiling does not render the fluid incapable of supporting life, as may be seen by removing the cotton-wool plug, when it will in a short time swarm with microbes.

Experiments conducted with these precautions all tell the

same tale: they prove conclusively that in properly sterilized putrescible infusions, adequately protected from the entrance of atmospheric germs, no micro-organisms ever make their appearance. So that the last argument for abiogenesis has been proved to be fallacious, and the doctrine of biogenesis shown, as conclusively as observation and experiment can show it, to be of universal application as far as existing conditions known to us are concerned.

It is also necessary to add that the presence of microbes in considerable quantities in our atmosphere has been proved experimentally. By drawing air through tubes lined with a solid nutrient material Prof. Percy Frankland showed that the air of South Kensington contains about thirty-five micro-organisms in every ten litres, and by exposing circular discs coated with the same substance he was further able to prove that in the same locality 279 micro-organisms fall upon one square foot of surface in one minute.

There is another question intimately connected with that of Biogenesis, although strictly speaking quite independent of it. It is a matter of common observation that, in both animals and plants, like produces like: that a cutting from a willow will never give rise to an oak, nor a snake emerge from a hen's egg. In other words, ordinary observation teaches the general truth of the doctrine of *Homogenesis*.

But there has always been a residuum of belief in the opposite doctrine of *Heterogenesis*, according to which the offspring of a given animal or plant may be something utterly different from itself, a plant giving rise to an animal or *vice versâ*, a lowly to a highly organised plant or animal and so on. Perhaps the most extreme case in which heterogenesis was once seriously believed to occur is that of

the "barnacle-geese." Buds of a particular tree growing near the sea were said to produce barnacles, and these falling into the water to develop into geese. This sounds absurd enough, but, within the last twenty years, two or three men of science have described, as the result of repeated observations, the occurrence of quite similar cases among microscopic organisms. For instance, the blood-corpuscles of the silkworm have been said to give rise to fungi, the protoplasm of the green weed Nitella (see Fig. 44) to Amœbæ and Infusoria (see p. 107), Euglenæ to thread-worms, and so on.

It is proverbially difficult to prove a negative, and it might not be easy to demonstrate, what all competent naturalists must be firmly convinced of, that every one of these supposed cases of heterogenesis is founded either upon errors of observation or upon faulty inductions from correct observations.

Let us take a particular case by way of example. Many years ago Dr. Dallinger observed among a number of Vorticellæ or bell-animalcules (Fig. 25) one which appeared to have become encysted upon its stalk. After watching it for some time, there was seen to emerge from the cyst a free-swimming ciliated Infusor called *Amphileptus*, not unlike a long-necked Paramœcium (Fig. 20, p. 108). Many observers would have put this down as a clear case of heterogenesis: Dallinger simply recorded the observation and waited. Two years later the occurrence was explained: he found the same two species in a pond, and watched an Amphileptus seize and devour a Vorticella, and, after finishing its meal, become encysted upon the stalk of its victim.

It is obvious that the only way in which a case of heterogenesis could be proved would be by actually watching the transformation, and this no heterogenist has ever done; at

the most, certain supposed intermediate stages between the extreme forms have been observed—say, between a Euglena and a thread-worm—and the rest of the process inferred. On the other hand, innumerable observations have been made on these and other organisms, the result being that each species investigated has been found to go through a definite series of changes in the course of its development, the ultimate result being invariably an organism resembling in all essential respects that which formed the starting-point of the observations: Euglenæ always giving rise to Euglenæ and nothing else, Bacteria to Bacteria and nothing else, and so on.

There are many cases which imperfect knowledge might class under heterogenesis, such as the origin of frogs from tadpoles or of jelly-fishes from polypes (Lesson XXII. Fig. 53), but in these and many other cases the apparently anomalous transformations have been found to be part of the normal and invariable cycle of changes undergone by the organism in the course of its development; the frog always gives rise ultimately to a frog, the jelly-fish to a jelly-fish. If a frog at one time produced a tadpole, at another a trout, at another a worm: if jelly-fishes gave rise sometimes to polypes, sometimes to Infusoria, sometimes to cuttle-fishes, and all without any regular sequence—*that* would be heterogenesis.

It is perhaps hardly necessary to caution the reader against the error that there is any connection between the theory of heterogenesis and that of organic evolution. It might be said—if, as naturalists tell us, dogs are descended from wolves and jackals and birds from reptiles, why should not, for instance, thread-worms spring from Euglenæ or Infusoria from Bacteria? To this it is sufficient to answer that the evolution of one form from another takes place by a series

of slow, orderly, progressive changes going on through a long series of generations (see Lesson XIII.); whereas heterogenesis presupposes the casual occurrence of sudden transformations in any direction—*i.e.*, leading to either a less or a more highly organized form—and in the course of a single generation.[1]

[1] Apart from such *continuous* variations, others, which may be described as *discontinuous*, do sometimes appear with apparent suddenness, but not to the extent which would be required by the theory of heterogenesis. —*W. N. P.*

LESSON X

PARAMŒCIUM, STYLONYCHIA, AND OXYTRICHA

It will have been noticed with regard to the simple unicellular organisms hitherto considered that all are not equally simple: that Protamœba (Fig. 2, p. 9) and Micrococcus (Fig. 15, p. 86) may be considered as the lowest of all, and that the others are raised above these forms in the scale of being in virtue of the possession of nucleus or contractile vacuole, or of flagella, or even, as in the case of Euglena (Fig. 5, p. 45), of a mouth or gullet.

Thus we may speak of any of the organisms already studied as relatively "high" or "low" with regard to the rest: the lowest or least differentiated forms being those which approach most nearly to the simplest conception of a living thing—a mere lump of protoplasm: the highest or most differentiated those in which the greatest complication of structure has been attained. It must be remembered, too, that this increase in structural complexity is always accompanied by some degree of division of physiological labour, or, in other words, that morphological and physiological differentiation go hand in hand.

We have now to consider certain organisms in which this differentiation has gone much further; which have, in fact,

acquired many of the characteristics of the higher animals and plants while remaining unicellular. The study of several of these more or less highly differentiated though unicellular forms will occupy the next seven Lessons.

It was mentioned above that, in the earlier stages of the putrefaction of an organic infusion, bacteria only were found, and that later, monads made their appearance. Still later organisms much larger than monads are seen, generally of an ovoidal form, moving about very quickly, and seen by the use of a high power to be covered with innumerable fine cilia. These are called *ciliate Infusoria*, in contradistinction to monads, which are often known as *flagellate Infusoria*: many kinds are common in putrefying infusions, some occur in the intestines of the higher animals, while others are among the commonest inhabitants of both fresh and salt water. Five genera of these Infusoria will form the subjects of this and the four following Lessons.

A very common ciliate infusor is the beautiful "slipper animalcule," *Paramæcium*, which from its comparatively large size and from the ease with which all essential points of its organization can be made out is a very convenient and interesting object of study.

Compared with the majority of the organisms which have come under our notice it may fairly be considered as gigantic, being no less than $\frac{1}{5}$—$\frac{1}{4}$ mm. (200—260μ) in length: in fact it is just visible to the naked eye as a minute whitish speck.

Its form (Fig. 20 A) can be fairly well imitated by making out of clay or stiff dough an elongated cylinder rounded at one end and bluntly pointed at the other; then giving the broader end a slight twist; and finally making on the side

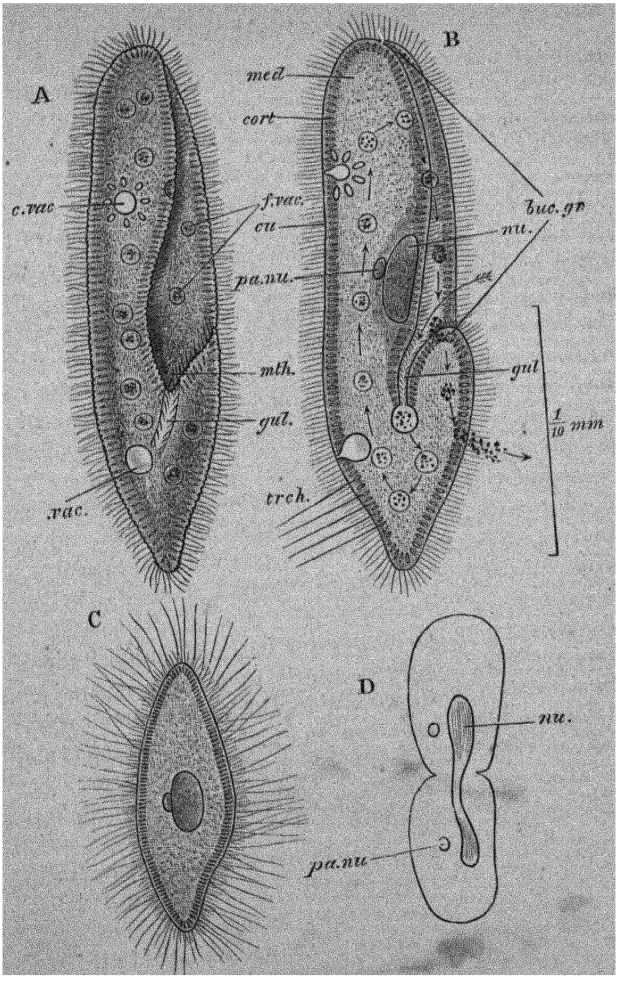

FIG. 20.—*Paramæcium caudatum.*

A, the living animal from the ventral aspect, showing the covering of cilia, the buccal groove (to the right) ending posteriorly in the mouth

(*mth*) and gullet (*gul*); several food vacuoles (*f. vac*), and the two contractile vacuoles (*c. vac*).

B, the same in optical sections showing cuticle (*cu*), cortex (*cort*), and medulla (*med*); buccal groove (*buc. gr*), mouth, and gullet (*gul*); numerous food vacuoles (*f. vac*) circulating in the direction indicated by the arrows, and containing particles of indigo, which are finally ejected at an anal spot; meganucleus (*nu*), micronucleus (*pa. nu*), and trichocysts, some of which (*trch*) are shown with their threads ejected.

The scale to the right of this figure applies to A and B.

C, a specimen killed with osmic acid, showing the ejection of trichocyst-threads, which project considerably beyond the cilia.

D, diagram of binary fission: the micronucleus (*pa. nu*) has already divided, the mega nucleus (*nu*) is in the act of dividing.

(D, after Lankester.)

rendered somewhat concave by the twist a wide shallow groove beginning at the broad end and gradually narrowing to about the middle of the body, where it ends in a tolerably deep depression.

The groove is called the *buccal groove* (Fig. 20, A & B, *buc. gr*): at the narrow end is a small aperture, the mouth (*mth*), which, like the mouth of Euglena (Fig. 5), leads into the soft internal protoplasm of the body. The surface of the creature on which the groove is placed is distinguished as the ventral surface, the opposite surface being upper or dorsal; the broad end is anterior, the narrow end posterior, the former being directed forwards as the animalcule swims. These descriptive terms being decided upon, it will be seen from Fig. 20 A, that the buccal groove begins on the left side of the body, and gradually curves over to the middle of the ventral surface.

As the animal swims its form is seen to be permanent, exhibiting no contractions of either an amœboid or a euglenoid nature. It is however distinctly flexible, often being bent in one or other direction when passing between obstacles such as entangled masses of weed. This permanence of contour is due to the presence of a tolerably firm though delicate cuticle (*cu*) which invests the whole surface.

The protoplasm thus enclosed by the cuticle is distinctly divisible into two portions—an external somewhat dense layer, the *cortical layer* or *cortex* (*cort*), and an internal more fluid material, the *medullary substance* or *medulla* (*med*). It will be remembered that a somewhat similar distinction of the protoplasm into two layers is exhibited by Amœba (p. 3), the ectosarc being distinguished from the endosarc simply by the absence of granules. In Paramœcium the distinction is a far more fundamental one: the cortex is radially striated and is comparatively firm and dense, while the medulla is granular and semi-fluid, as may be seen from the fact that food particles (*f. vac*, see below, p. 112) move freely in it, whereas they never pass into the cortex. The medulla has a reticular structure similar to that of the protoplasm of the ordinary animal cell (Fig. 9, p. 62), consisting of a delicate granular network the meshes of which are filled with a transparent material. In the cortex the meshes of the network are closer, and so form a comparatively dense substance. The cortex also exhibits a superficial oblique striation, forming what is called the *myophan layer*.

The mouth (*mth*) leads into a short funnel-like tube, the gullet (*gul*), which is lined by cuticle and passes through the cortex to end in the s[redacted]edulla, thus making a free communication between t[redacted]rnal water.

The cilia with wh[redacted]e of approximately equal size, quite short[redacted]to the entire animal, and arranged in longitudinal rows over [redacted] whole outer surface. They consist of prolongations of t[redacted]tex, and each passes through a min[redacted]uticle. They are in con[redacted]thereby distinguished fr[redacted]occus, Euglena, &c., which exhib[redacted]more or less intermittent lashing movements (see p. 25, note, and p. 59). Their rapid motion and

minute size make them somewhat difficult to see while the Paramœcium is alive and active, but after death they are very obvious, and look quite like a thick covering of fine silky hairs.

Near the middle, and close to the cortex, is a large oval nucleus (B, *nu*), which is peculiar in taking on a uniform tint when stained, showing none of the distinction into chromatin and nuclear sap which is so marked a feature in many of the nuclei we have studied (see especially Fig. 1, p. 2, and Fig. 9, p. 62). It has also a further peculiarity: against one side of it in *P. caudatum* is a small oval structure (*pa. nu*) which is also deeply stained by magenta or carmine. This is the *micronucleus*: it is to be considered as a second, smaller nucleus, the larger body being distinguished as the *meganucleus*. In the closely allied *P. aurelia*, there are two micronuclei.

There are two contractile vacuoles (*c. vac*), one situated at about a third of the entire length from the anterior end of the body, the other at about the same distance from the posterior end: they are in relation with the cortex.

The action of the contractile vacuoles is very beautifully seen in a Paramœcium at rest: it is particularly striking in a specimen subjected to slight pressure under a cover glass, but is perfectly visible in one which has merely temporarily supended its active swimming movements. It is then seen that during the *diastole*, or phase of expansion of each vacuole, a number—about six to ten—of delicate radiating, spindle-shaped spaces filled with fluid appear round it, like the rays of a star (upper vacuole in A & B): the vacuole itself contracts or performs its *systole*, completely disappearing from view, and immediately afterwards the radiating canals flow together and re-fill it, becoming themselves emptied and therefore invisible for an instant (lower vacuole in A & B) but rapidly

appearing once more. There seems to be no doubt that the water taken in with the food is collected into these canals, emptied into the vacuole, and finally discharged into the surrounding medium.

The process of feeding can be very conveniently studied in Paramœcium by placing in the water some finely-divided carmine or indigo. When the creature comes into the neighbourhood of the coloured particles, the latter are swept about in various directions by the action of the cilia: some of them are however certain to be swept into the neighbourhood of the buccal groove and gullet, the cilia of which all work downwards, *i.e.* towards the inner end of the gullet. The grains of carmine are thus carried into the gullet, where for an instant they lie surrounded by the water of which it is full: then, instantaneously, probably by the contraction of the tube itself, the animalcule performs a sort of gulp, and the grains with an enveloping globule of water or food-vacuole are forced into the medullary protoplasm. This process is repeated again and again, so that in any well-nourished Paramœcium there are to be seen numerous globular spaces filled with water and containing particles of food—or in the present instance of carmine or indigo. At every gulp the newly formed food-vacuole pushes, as it were, its predecessor before it: contraction of the medullary protoplasm also takes place in a definite direction, and thus a circulation of food-vacuoles is produced, as indicated in Fig. 20, B, by arrows.

After circulating in this way for some time the water of the food-vacuoles is gradually absorbed, being ultimately excreted by the contractile vacuoles, so that the contained particles come to lie in the medulla itself (refer to figure). The circulation still continues, until finally the particles are brought to a spot situated about half-way between the mouth and the posterior end of the body: here if carefully watched they

are seen to approach the surface and then to be suddenly ejected. The spot in question is therefore to be looked upon as a potential *anus*, or aperture for the egestion of fæces or undigested food-matters. It is a potential and not an actual anus, because it is not a true aperture but only a soft place in the cortex through which, by the contractions of the medulla, solid particles are easily forced.

Of course when Paramœcium ingests, as it usually does, not carmine but minute living organisms, the latter are digested as they circulate through the medullary protoplasm, and only the non-nutritious parts cast out at the anal spot. It has been found by experiment that this infusor can digest not only proteids but also starch and perhaps fats. The starch is probably converted into *dextrin*, a carbohydrate having the same formula ($C_6H_{10}O_5$) but soluble and diffusible. Oils or fats seem to be partly converted into fatty acids and glycerine. The nutrition of Paramœcium is therefore characteristically holozoic.

It was mentioned above (p. 110) that the cortex is radially striated in optical section. Careful examination with a very high power shows that this appearance is due to the presence in the cortex of minute spindle-shaped bodies (B and C, *trch*) closely arranged in a single layer and perpendicular to the surface. These are called *trichocysts*.

When a Paramœcium is killed, either by the addition of osmic acid or some other poisonous reagent or by simple pressure of the cover glass, it frequently assumes a remarkable appearance. Long delicate threads suddenly appear, projecting from its surface in all directions (C) and looking very much as if the cilia had suddenly protruded to many times their original length. But these filaments have really nothing to do with the cilia; they are contained under ordinary circumstances in the trichocysts, probably coiled up;

and by the contraction of the cortex consequent upon any sudden irritation they are projected in the way indicated. In Fig. 20 B, a few trichocysts (*trch*) are shown in the exploded condition, *i.e.* with the threads protruded. Most likely these bodies are weapons of offence like the very similar structures (nematocysts) found in polypes (see Lesson XXI. Figs. 50 and 51).

Paramœcium multiplies by simple fission, the division of the body being always preceded by the elongation and subsequent division of the mega- and micronucleus (Fig. 20, D). Division of the meganucleus is direct, that of the micronucleus indirect, *i.e.* takes place by mitosis.

Conjugation also occurs, usually after multiplication by fission has gone on for some time, but the details and the results of the process are very different from what are found to obtain in Heteromita (p. 41). Two Paramœcia come into contact by their ventral faces (Fig. 21, A) and the meganucleus (*mg. nu*) of each gradually breaks up into minute fragments (D—G) which are either absorbed into the protoplasm or ejected. At the same time the micronucleus (*mi. nu*) divides, by mitosis, and the process is repeated, the result being that each gamete contains four micronuclei (B). Two of these become absorbed and disappear (C, *mi. nu'*, *mi. nu''*) ; of the remaining two one is now distinguished as the *active pronucleus*, the other as the *stationary pronucleus*. Next, the active pronucleus of each gamete passes into the body of the other (C) and fuses with its stationary pronucleus (D) : in this way each gamete contains a single nuclear body, the *conjugation-nucleus* (E), formed by the union of two similar pronuclei one of which is derived from another individual. It is this fusion of two nuclear bodies, one from each of the con-

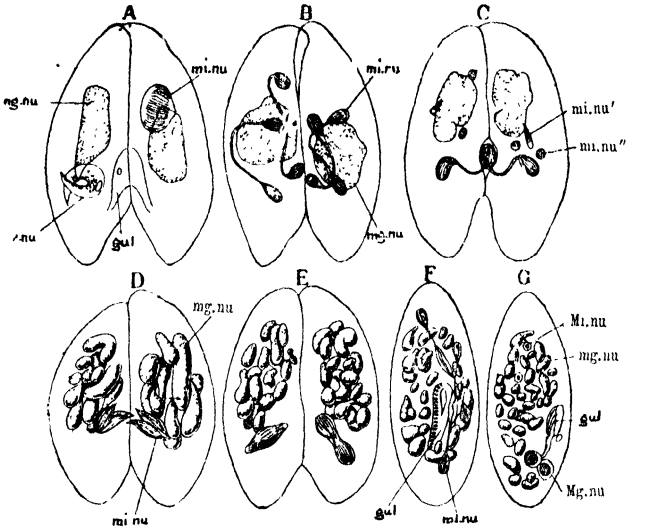

FIG. 21.—*Stages in the Conjugation of Paramœcium.*

A, Commencement of conjugation: the meganuclei (*mg. nu*) of the two gametes are almost unaltered: the micronuclei (*mi. nu*) are in an early stage of mitosis: *gul*, gullet.

B, The micronuclei have divided twice, each gamete now containing four.

C, Two of the micronuclei (*mi. nu'*, *mi. nu"*) of each gamete are degenerating: of the remaining two, one—the active pronucleus—is passing into the other gamete.

D, The active pronucleus of each gamete has passed into the other gamete and is conjugating with its stationary pronucleus. The meganucleus (*mg. nu*) has begun to break up.

E, Each gamete contains a single conjugation-nucleus formed by the union of its own stationary pronucleus with the active pronucleus of the other gamete. On the right side the conjugation-nucleus is beginning to divide.

F, Conjugation is over and only one of the separated gametes is shown. It contains the fragments of the meganucleus (dotted) and four nuclear bodies (*mi. nu*) produced by the division and redivision of the conjugation-nucleus.

G, Two of the products of division of the conjugation-nucleus (*Mg. nu*) are enlarging to form meganuclei, the other two (*Mi. nu*) are taking on the characters of micronuclei. Fragments of the original meganucleus (*mg. nu.*) still remain.

(After Hertwig.)

jugating cells, which is the essential part of the whole process. Soon after this the gametes separate from one another and begin once more to lead an independent existence; the conjugation nucleus of each undergoes a twice repeated process of division, the infusor thus acquiring four small nuclei (F). Two of these enlarge and take on the character of meganuclei (G, *Mg. nu*), the other two remaining unaltered and having the character of micronuclei (*Mi. nu*). Thus shortly after the completion of conjugation each individual contains two mega- and two micronuclei all derived from the conjugation-nucleus. Ordinary transverse fission now takes place, as described in the preceding paragraph, each of the two daughter-cells having one mega- and one micronucleus, and thus the normal form of the species is re-acquired.

It will be noticed that, in the present instance, conjugation is not a process of multiplication: it has been ascertained that during the time two infusors are conjugating each might have produced several thousand offspring by continuing to undergo fission at the usual rate. The importance of the process lies in the exchange of nuclear material between the two conjugating individuals: without such exchange these organisms have been said to undergo a gradual process of senile decay characterised by diminution in size and degeneration in structure.

Another ciliated infusor common in stagnant water and organic infusions is *Stylonychia mytilus*, an animalcule varying from $\frac{1}{10}$mm. to $\frac{1}{5}$mm.

Like Paramœcium it is often to be seen swimming rapidly in the fluid, but unlike that genus it frequently creeps about, almost like a wood-louse or a caterpillar, on the surface of the plants or other solid objects among which it lives.

In correspondence with this, instead of being nearly cylindrical, it is flattened on one—the ventral—side, and is thus irregularly plano-convex in transverse section (Fig. 22, c).

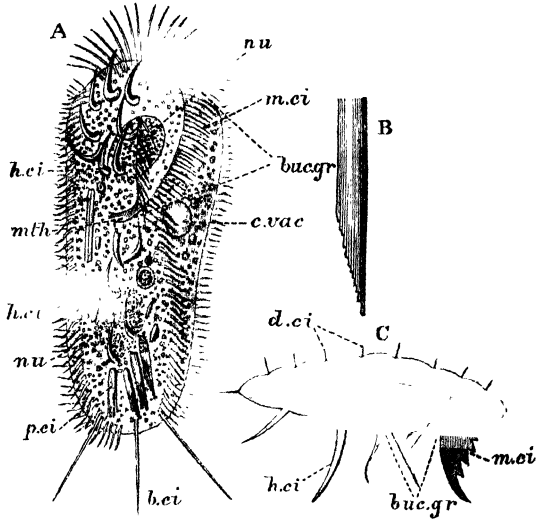

FIG. 22.—A, *Stylonychia mytilus*, ventral aspect, showing the buccal groove (*buc. gr.*) and mouth (*mth*), two nuclei (*nu*, *nu*), contractile vacuole (*c. vac*), and cilia differentiated into hook-like (*h. ci*), bristle-like (*b. ci*), plate-like (*p. ci*), and fan-like (*m. ci*) organs.

B, one of the plate-like cilia of the same (*p. ci* in A), showing its frayed extremity.

C, transverse section of *Gastrostyla*, a form allied to Stylonychia, showing buccal groove (*buc. gr.*), small dorsal cilia (*d. ci*), hook-like cilium (*h. ci*), and the various cilia of the buccal groove, including an expanded fan-like organ (*m. ci*). A and B after Claparède and Lachmann: C after Sterki.

It resembles Paramœcium in general structure (compare Fig. 22, A, with Fig. 20, A); but owing to the absence of trichocysts the distinction between cortex and medulla is

less obvious: moreover, it has two mega nuclei (*nu*) and only one contractile vacuole (*c vac*)

But it is in the character of its cilia that Stylonychia is most markedly distinguished from Paramœcium: these structures, instead of being all alike both in form and size, are modified in a very extraordinary way.

On the dorsal surface the cilia are represented only by very minute processes of the cuticle (c, *d. ci*) set in longitudinal grooves and exhibiting little movement. It seems probable that these are to be looked upon as *vestigial* or *rudimentary* cilia, *i.e.*, as the representatives of cilia which were of the ordinary character in the ancestors of Stylonychia, but which have undergone partial *atrophy*, or diminution beyond the limits of usefulness, in correspondence with the needs of an animalcule which has taken to creeping on its ventral surface, instead of swimming freely and so using all its cilia equally.

On the other hand, the cilia on the ventral surface have undergone a corresponding enlargement or *hypertrophy*. Near the anterior and posterior ends and about the middle are three groups of cilia of comparatively immense size, shaped either like hooks (*h. ci.*), or like flattened rods frayed at their ends (*p. ci*, and B). All these structures neither vibrate rhythmically like ordinary cilia nor perform lashing movements like flagella, but move at the base only, like single-jointed legs. The movement is under the animal's control, so that it is able to creep about by the aid of these hooks and plates in much the same way as a caterpillar by means of its legs.

Notice that we have here a third form of contractility: in amœboid movement there is an irregular flowing of the protoplasm (pp. 4 and 9); in ciliary movement a flexion of a protoplasmic filament from side to side (p. 33); while

in the present case we have sudden contractions taking place at irregular intervals. The movements of these locomotor hooks and plates are therefore very similar to the muscular contractions to which the movements of the higher animals are due: it cannot be said that definite muscles are present in Stylonychia, but the protoplasm in certain regions of the unicellular body is so modified as to be able to perform a sudden contraction in a definite direction. The nature of muscular contraction will be further discussed in the next Lesson (see p. 130).

The remainder of the ventral surface, with the exception of the buccal groove, is bare, but along each side of the margin is a row of large vibratile cilia, of which three at the posterior end are modified into long, stiff, bristle-like processes (A, *b. ci*).

There is also a special differentiation of the cilia of the buccal groove (*buc. gr.*). On its left side is a single row of very large and powerful cilia (A and C, *m. ci*) which are the chief organs for causing the food-current as well as the main swimming-organs: each has the form of a triangular fan-like plate (C, *m. ci*). On the right side of the buccal groove is a row of smaller but still large cilia of the ordinary form, and in the interior of the gullet a row of extremely delicate cilia which aid in forcing particles of food down the gullet into the medulla.

In Stylonychia and allied genera intermediate forms are found between these peculiar hooks, plates, bristles, and fans, and ordinary cilia; from which we may conclude that these diverse appendages are to be looked upon as highly modified or *differentiated* cilia. Probably they have been evolved in the course of time from ordinary cilia, and on the principle that the more complicated or specialized organisms are descended from simpler or more generalized

forms (see Lesson XIII.), we may consider Stylonychia as the highly-specialized descendant of some uniformly-ciliated progenitor.

A third genus of ciliated Infusoria must be referred to in concluding the present Lesson. We have seen how the nucleus of a Paramœcium which has just conjugated breaks up and apparently disappears (Fig. 21, A—G). In *Oxytricha*, a genus closely resembling Stylonychia, the two nuclei have been found to break up into a large number of minute granules (Fig 23), which can be seen only after

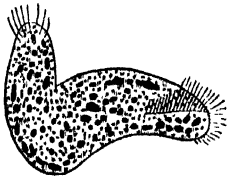

FIG. 23.—*Oxytricha flava*, killed and stained, showing the fragmentation of the nuclei. (After Gruber.)

careful staining and by the use of high magnifying powers. This process is called *fragmentation* of the nucleus; in other cases it goes even further, and the nucleus is reduced to an almost infinite number of chromatin granules only just visible under the highest powers. From this it seems very probable that organisms which, like Protamœba (p. 9) and Protomyxa (p. 49), appear non-nucleate, are actually provided with a nucleus in this pulverized condition, and that a nucleus in some form or other is an essential constituent of the cell.

LESSON XI

OPALINA

THE large intestine of the common frog often contains numbers of ciliate Infusoria belonging to two or three genera. One of these parasitic animalcules, called *Opalina ranarum*, will now be described. It is easily obtained by killing a frog, opening the body, making an incision in the rectum, and spreading out a little of its blackish contents in a drop of water on a slide.

Opalina has a flattened body with an oval outline (Fig. 24, A, B), and full-sized specimens may be as much as one millimetre in length. The protoplasm is divided into cortex and medulla and is covered with a cuticle, and the cilia are equal-sized and uniformly arranged in longitudinal rows over the whole surface (A).

On a first examination no nucleus is apparent, but after staining a large number of nuclei can be seen (B, *nu*), each being a globular body (C, 1), consisting of a nuclear matrix surrounded by a membrane and containing a coil or network of chromatin. These nuclei multiply within the body of the infusor, and in so doing pass through the various changes characteristic of mitosis or indirect nuclear division

(compare Fig. 10, p. 64, with Fig. 24, c): the chromatin

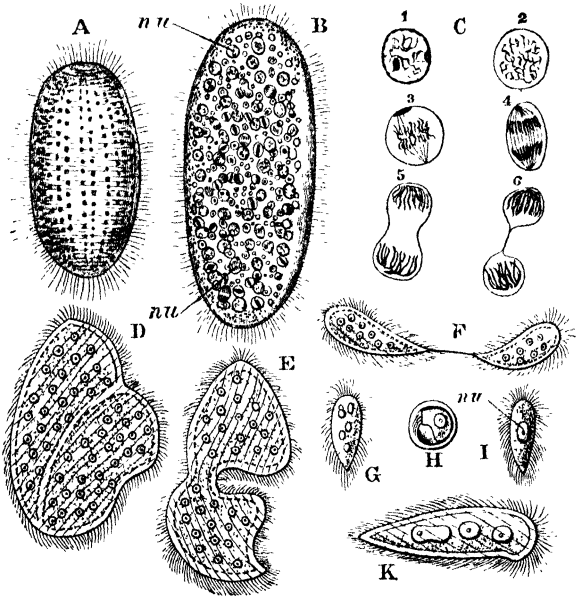

FIG. 24.—*Opalina ranarum.*

A, living specimen, surface view, showing longitudinal rows of cilia.

B, the same, stained, showing numerous nuclei (*nu*) in various stages of division.

C, 1—6, stages in nuclear division.

D, longitudinal fission.

E, transverse fission.

F, the same in a specimen reduced in size by repeated division.

G, final product of successive divisions.

H, encysted form.

I, uninucleate form produced from cyst.

K, the same after multiplication of the nucleus has begun.

(A—C, after Pfitzner; D—K, from Saville Kent, after Zeller.)

breaks up (C, 2), a spindle is formed with the chromosomes across its equator (3), the chromosomes pass to the poles of

the spindle (4, 5), and the nucleus becomes constricted (5) and finally divides into two (6).

The presence of numerous nuclei in Opalina is a fact worthy of special notice. The majority of the organisms we have studied are uninucleate as well as unicellular: the higher animals and plants we found (Lesson VI.) to consist of numerous cells each with a nucleus: Opalina, on the other hand, is multinucleate but its protoplasm is undivided, so that it presents a condition of things intermediate between the unicellular and the multicellular types of structure: it is most suitably described as *non-cellular*. An approach to this condition is seen in Stylonychia, which is unicellular and binucleate; but apart from *Amœba quarta*, the only organisms we have yet studied in which numerous nuclei of the ordinary character occur in an undivided mass of protoplasm are the Mycetozoa (p. 52), and in them the multinucleate condition of the plasmodium is largely due to its being formed by the fusion of separate cells, while in Opalina it is due, as we shall see, to the repeated binary fission of an originally single nucleus.

There is no contractile vacuole, and no trace of either mouth or gullet, so that the ingestion of solid food is impossible. The creature lives, as already stated, in the intestine of the frog: it is therefore an *internal parasite*, or *endo-parasite*, having the frog as its *host*. The intestine contains the partially-digested food of the frog, and it is by the absorption of this that the Opalina is nourished. Having no mouth, it feeds solely by imbibition: whether it performs any kind of digestive process itself is not certainly known, but the analogy of other mouthless parasites leads us to expect that it simply absorbs food ready digested by its host, upon which it is dependent for a constant supply of soluble and diffusible nutriment..

Thus Opalina, in virtue of its parasitic mode of life, is

saved the performance of certain work—the work of digestion, that work being done for it by its host. This is the essence of internal parasitism : an organism exchanges a free life, burdened with the necessity of finding food for itself, for existence in the interior of another organism, on which, in one way or another, it levies blackmail.

Note the close analogy between the nutrition of an internal parasite like Opalina and the saprophytic nutrition of a monad (p. 39). In both the organism absorbs proteids rendered soluble and diffusible, in the one case by the digestive juices of the host. in the other by the action of putrefactive bacteria.

The reproduction of Opalina presents certain points of interest, largely connected with its peculiar mode of life. It is obvious that if the Opalinæ simply went on multiplying, by fission or otherwise, in the frog's intestine, the population would soon outgrow the means of subsistence : moreover, when the frog died there would be an end of the parasites. What is wanted in this as in other internal parasites is some mode of multiplication which shall serve as a *means of dispersal*, or in other words, enable the progeny of the parasite to find their way into the bodies of other hosts, and so start new colonies instead of remaining to impoverish the mother-country.

Opalina multiplies by a somewhat peculiar process of binary fission : an animalcule divides in an oblique direction (Fig. 24, D), and then each half, instead of growing to the size of the parent cell, divides again transversely (E). The process is repeated again and again (F), the plane of division being alternately oblique and transverse, until finally small bodies are produced (G), about $\frac{1}{20}$–$\frac{1}{30}$ mm. in length, and containing two to four nuclei.

If the parent-cell had divided simultaneously into a num-

ber of these little bodies the process would have been one of multiple fission : as it is, it forms an interesting link between simple and multiple fission.

Opalina ranarum multiplies in this way in the spring—*i.e.* during the frog's breeding season. Each of the small products of division (G) becomes encysted (H), and in this passive condition is passed out with the frog's excrement, probably falling on to a water-weed or other aquatic object. Nothing further takes place unless the cyst is swallowed by a tadpole, as must frequently happen when these creatures, produced in immense numbers from the frogs' eggs, browse upon the water-weeds which form their chief food.

Taken into the tadpole's intestine, the cyst is burst or dissolved, and its contents emerge as a lanceolate mass of protoplasm (I), containing a single nucleus and covered with cilia. This, as it absorbs the digested food in the intestine of its host, grows, and at the same time its nucleus divides repeatedly (K) in the way already described, until by the time the animalcule has attained the maximum size it has also acquired the large number of nuclei characteristic of the genus.

Here, then, we have another interesting case of development (see p. 43) : the organism begins life as a very small uninucleate mass of protoplasm, and, as it increases in size, increases also in complexity by the repeated binary fission of its nucleus.

LESSON XII

VORTICELLA AND ZOOTHAMNIUM

THE next organism we have to consider is a ciliated infusor even commoner than those described in the two previous lessons. It is hardly possible to examine the water of a pond with any care without finding in it, sometimes attached to weeds, sometimes to the legs of water-fleas, sometimes to the sticks and stones of the bottom, numbers of exquisitely beautiful little creatures, each like an inverted bell with a very long handle, or a wine-glass with a very long stem. These are the well-known "bell-animalcules;" the commonest among them belong to various species of the genus *Vorticella*.

The first thing that strikes one about Vorticella (Fig. 25, A) is the fact that it is permanently fixed, like a plant, the *proximal* or near end of the stalk being always firmly fixed to some aquatic object, while to the *distal* or far end the body proper of the animalcule is attached.

But in spite of its peculiar form it presents certain very obvious points of resemblance to Paramœcium, Stylonychia, and Opalina. The protoplasm is divided into cortex (Fig. 25, C, *cort*) and medulla (*med*), and is invested with a

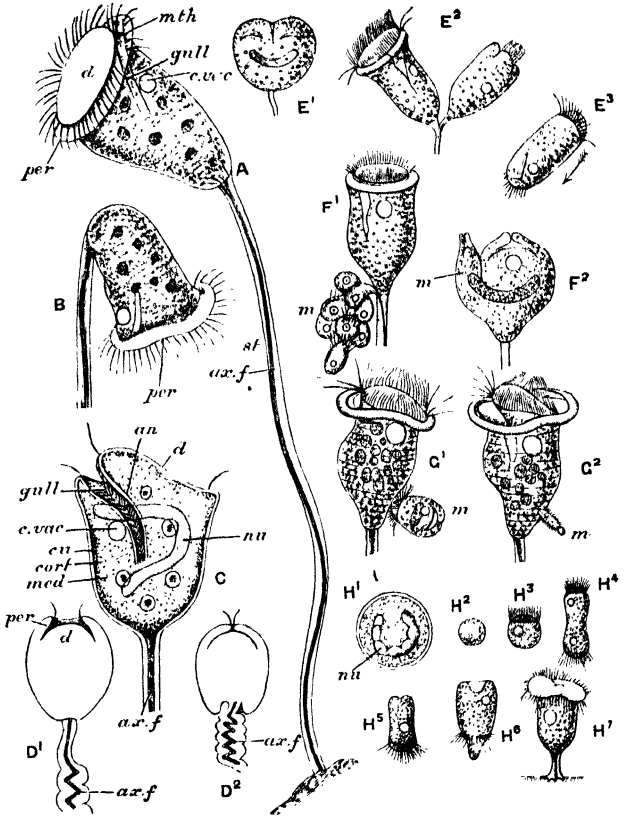

FIG. 25.—*Vorticella.*

A, living specimen fully expanded, showing stalk (*st*) with axial fibre (*ax. f*), peristome (*per*), disc (*d*), mouth (*mth*), gullet (*gull*), and contractile vacuole (*c. vac*).

B, the same, bent on its stalk and with the disc turned away from the observer.

C, optical section of the same, showing cuticle (*cu*), cortex (*cort*), medulla (*med*), nucleus (*nu*), gullet (*gull*), several food-vacuoles, and anus (*an*), as well as the structures shown in A.

D¹, a half-retracted and D² a fully-retracted specimen, showing the coiling of the stalk and overlapping of the disc by the peristome.

E^1, commencement of binary fission; E^2, completion of the process; E^3, the barrel-shaped product of division swimming freely in the direction indicated by the arrow.

F^1, a specimen dividing into a megazooid and several microzooids (*m*); F^2, division into one mega- and one microzooid.

G^1, G^2, two stages in conjugation showing the gradual absorption of the microgamete (*m*) into the megagamete.

H^1, multiple fission of encysted form, the nucleus dividing into numerous masses: H^2, spore formed by multiple fission; H^3 – H^7, development of the spore; H^4 is undergoing binary fission.

(E—H after Saville Kent.)

delicate cuticle (*cu*). There is a single contractile vacuole (*c. vac*) the movements of which are very readily made out owing to the ease with which the attached organism is kept under observation. There is a meganucleus (*nu*) remarkable for its elongated band like form, and having in its neighbourhood a small rounded micronucleus. Cilia are also present, but the way in which they are disposed is very peculiar and characteristic. To understand it we must study the form of the body a little more closely.

The conical body is attached by its apex or proximal end to the stalk: its base or distal end is expanded so as to form a thickened rim, the *peristome* (*per*), within which is a plate-like body elevated on one side, called the *disc* (*d*) and looking like the partly raised lid of a chalice. Between the raised side of the disc and the peristome is a depression, the mouth (*mth*), leading into a conical gullet (*gull*).

There is reason for thinking that the whole proximal region of Vorticella answers to the ventral surface of Paramœcium, and its distal surface with the peristome and disc to the dorsal surface of the free-swimming genus: the mouth is to the left in both.

A single row of cilia is disposed round the inner border of the peristome, and continued on the one hand down the gullet, and on the other round the elevated portion of the

disc ; the whole row of cilia thus takes a spiral direction. The rest of the body is completely bare of cilia.

The movements of the cilia produce a very curious optical illusion : as one watches a fully-expanded specimen it is hardly possible to believe that the peristome and disc are not actually revolving—a state of things which would imply that they were discontinuous from the rest of the body. As a matter of fact the appearance is due to the successive contraction of all the cilia in the same direction, and is analogous to that produced by a strong wind on a field of corn or long grass. The bending down of successive blades of grass produces a series of waves travelling across the field in the direction of the wind. If instead of a field we had a large circle of grass, and if this were acted upon by a cyclone, the wave would travel round the circle, which would then appear to revolve.

Naturally the movement of the circlet of cilia produces a small whirlpool in the neighbourhood of the Vorticella, as can be seen by introducing finely-powdered carmine into the water. It is through the agency of this whirlpool that food particles are swept into the mouth, surrounded, as in Paramœcium, by a globule of water : the food-vacuoles (*f. vac*) thus constituted circulate in the medullary protoplasm, and the non-nutritive parts are finally egested at an anal spot (*an*) situated near the base of the gullet.

The stalk (*st*) consists of a very delicate, transparent, outer substance, which is continuous with the cuticle of the body and contains a delicate *axial fibre* (*ax. f.*) running along it from end to end in a somewhat spiral direction. This fibre is a prolongation of the cortex of the body (c, *ax. f.*) : under a very high power it appears granular or delicately striated, the striæ being continued into the cortex of the proximal part of the body.

A striking characteristic of Vorticella is its extreme irritability, *i.e.*, the readiness with which it responds to any external stimulus (see p. 10). The slightest jar of the microscope, the contact of some other organism, or even a current of water produced by some free-swimming form like Paramœcium, is felt directly by the bell-animalcule, and is followed by an instantaneous change in the relative position of its parts. The stalk becomes coiled into a close spiral (D^1, D^2) so as to have a mere fraction of its original length, and the body from being bell-shaped becomes globular, the disc being withdrawn and the peristome closed over it (D^1, D^2).

The coiling of the stalk leads us to the consideration of the particular form of contractility called *muscular*, which we have already met with in Stylonychia (p. 118). It was mentioned above that while the stalk in its fully expanded condition is straight, the axial fibre is not straight, but forms a very open spiral, *i.e.*, it does not lie in the centre of the stalk but at any transverse section is nearer the surface at one spot than elsewhere, and this point as we ascend the stalk is directed successively to all points of the compass.

Now suppose that the axial fibre undergoes a sudden contraction, that is to say, a decrease in length accompanied by an increase in diameter, since as we have already seen (p. 10) there is no decrease in volume in protoplasmic contraction. There will naturally follow a corresponding shortening of the elastic cuticular substance which forms the outer layer of the stalk. If the axial fibre were entirely towards one side of the stalk, the result of the contraction would be a flexure of the stalk towards that side, but, as its direction is spiral, the stalk is bent successively in every direction, that is, is thrown into a close spiral coil.

The axial fibre is therefore a portion of the protoplasm which possesses the property of contractility in a special

degree; in which moreover contraction takes place in a definite direction—the direction of the length of the fibre—so that its inevitable result is to shorten the fibre and consequently to bring its two ends nearer together. This is the essential characteristic of a muscular contraction, and the axial fibre in the stalk of Vorticella is therefore to be looked upon as the first instance of a clearly differentiated *muscle* which has come under our notice.

There are some interesting features in the reproduction of Vorticella. It multiplies by binary fission, dividing through the long axis of the body (Fig. 25, E^1, E^2). Hence it is generally said that fission is longitudinal, not transverse, as in Paramœcium. But on the theory (p. 128) that the peristome and disc are dorsal and the attached end ventral, fission is really transverse in this case also.

It will be seen from the figures that the process takes place by a cleft appearing at the distal end (E^1), and gradually deepening until there are produced two complete and full-sized individuals upon a single stalk (E^2). This state of things does not last long: one of the two daughter-cells takes on a nearly cylindrical form, keeps its disc and peristome retracted, and acquires a new circlet of cilia near its proximal end (E^3): it then detaches itself from the stalk, which it leaves in the sole possession of its sister-cell, and swims about freely for a time in the direction indicated by the arrow. Sooner or later it settles down, becomes attached by its proximal end, loses its basal circlet of cilia, and develops a stalk, which ultimately attains the normal length.

The object of this arrangement is obvious. If when a Vorticella divided, the plane of fission extended down the stalk until two ordinary fixed forms were produced side by side, the constant repetition of the process would so increase

the numbers of the species in a given spot that the food-supply would inevitably run short. This is prevented by one of the two sister-cells produced by fission leading a free existence long enough to enable it to emigrate and settle in a new locality, where the competition with its fellows will be less keen. The production of these free-swimming zooids is therefore a means of dispersal (see p. 124): contrivances having this object in view are a very general characteristic of fixed as of parasitic organisms.

Conjugation occasionally takes place, and presents certain peculiarities. A Vorticella divides either into two unequal halves (F^2) or into two equal halves, one of which divides again into from two to eight daughter-cells (F^1). There are thus produced from one to eight *microzooids* which resemble the barrel-shaped form (F^3) in all but size, and like it become detached and swim freely by means of a basal circlet of cilia. After swimming about for a time, one of these microzooids comes in contact with an ordinary form or *megazooid*, when it attaches itself to it near the proximal end (G^1), and under goes gradual absorption (G^2), the mega- and microzooids becoming completely and permanently fused. As in Paramœcium, conjugation is followed by increased activity in feeding and dividing (p. 116).

Notice that in this case the conjugating bodies or gametes are not of equal size and similar characters, but one, which is conveniently distinguished as the *microgamete* (= microzooid) is relatively small and active, while the other or *megagamete* (= megazooid, or ordinary individual) is relatively large and passive. As we shall see in a later lesson, this differentiation of the gametes is precisely what we get in almost all organisms with two sexes: the microgamete being the male, the megagamete the female conjugating body (see p. 173).

The result of conjugation is strikingly different in the three cases already studied: in Heteromita (p. 41) the two gametes unite to form a zygote, a motionless body provided with a cell-wall, the protoplasm of which divides into spores: in Paramœcium (p. 114) no zygote is formed, conjugation being a mere temporary union: in Vorticella the zygote is an actively moving and feeding body, indistinguishable from an ordinary individual of the species.

Vorticella sometimes encysts itself (Fig. 25, H[1]), and the nucleus of the encysted cell has been observed to break up into a number of separate masses, each doubtless surrounded by a layer of protoplasm. After a time the cyst bursts, and a number of small bodies or spores (H[2]) emerge from it, each containing one of the products of division of the nucleus. These acquire a circle of cilia (H[3]), by means of which they swim freely, and they are sometimes found to multiply by simple fission (H[4]). Finally, they settle down (H[5]) by the end at which the cilia are situated, the attached end begins to elongate into a stalk (H[6]), this increases in length, the basal circlet of cilia is lost, and a ciliated peristome and disc are formed at the free end (H[7]). In this way the ordinary form is assumed by a process of development recalling that which we found to occur in Heteromita (p. 43), but with an important difference: the free-swimming young of Vorticella (H[3]), to which the spores formed by division of the encysted protoplasm give rise, differ strikingly in form and habits from the adult. This is expressed by saying that development is in this case accompanied by a *metamorphosis*, this word, literally meaning simply a change, being always used in biology to express a striking and fundamental difference in form and habit between the young and the adult; as, for instance, between the tadpole and the frog, or between the caterpillar and the butterfly. It is obvious

that in the present instance metamorphosis is another means of ensuring dispersal.

In Vorticella, as we have seen, fission results not in the

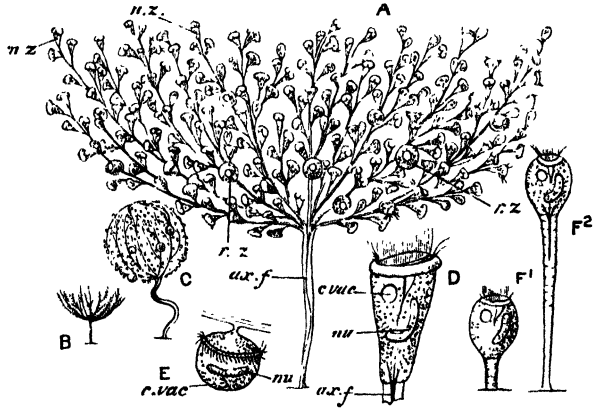

FIG. 26.—*Zoothamnium arbuscula.*

A, entire colony, magnified, showing nutritive (*n. z*) and reproductive (*r. z*) zooids ; *ax. f* axial fibre of the stem.

B, the same, natural size.

C, the same, magnified, in the condition of retraction.

D, nutritive zooid, showing nucleus (*nu*), contractile vacuole (*c. vac*), gullet, and axial fibre (*ax. f*).

E, reproductive zooid, showing nucleus (*nu*) and contractile vacuole (*c. vac*), and absence of mouth and gullet.

F^1, F^2, two stages in the development of the reproductive zooid. (After Saville Kent.)

production of equal and similar daughter-cells, but of one stalked and one free-swimming form. It is however quite possible to conceive of a Vorticella-like organism in which the parent cell divides into two equal and similar products, each retaining its connection with the stalk. If this process were repeated again and again, and if, further, the plane of

fission were extended downwards so as to include the distal end of the stalk, the result would be a branched, tree-like stem with a Vorticella-like body at the end of every branch.

As a matter of fact, this process takes place not in Vorticella itself, but in a nearly allied infusor, the beautiful *Zoothamnium*, a common genus found mostly in sea-water attached to weeds and other objects.

Zoothamnium arbuscula (Fig. 26, A) consists of a main stem attached by its proximal end and giving off at its distal end several branches, on each of which numerous shortly-stalked bell-animalcules are borne, like foxgloves or Canterbury-bells on their stem. The entire tree is about 1 cm. high, and so can be easily seen by the naked eye: it is shown of the natural size in Fig. 26, B.

We see, then, that Zoothamnium differs from all our previous types in being a *compound organism*. The entire "tree" is called a *colony* or *stock*, and each separate bell-animalcule borne thereon is an *individual* or *zooid*, morphologically equivalent to a single Vorticella or Paramœcium.

As in Vorticella, the stem consists of a cuticular sheath with an axial muscle-fibre (*ax. f*), which, at the distal end of the main stem, branches, like the stem itself, a prolongation of it being traceable to each zooid (D). So that the muscular system is common to the whole colony, and any shock causes a general contraction, the tree-like structure assuming an almost globular form (C).

It will be noticed from the figure that all the zooids of the colony are not alike: the majority are bell-shaped and resemble Vorticellæ (A, *n. z*, and D), but here and there are found larger bodies (A, *r. z*, and E) of a globular form, without mouth, peristome, or disc, and with a basal circlet of cilia. The characteristic band-like nucleus (*nu*) and the

contractile vacuole (*c. vac*) are found in both the bell-shaped and the globular zooids.

It is to these globular, mouthless zooids that the functions of reproducing the whole colony and of ensuring dispersal are assigned. They become detached, swim about freely for a time, then settle down, develop a stalk and mouth (F^1, F^2), and finally, by repeated fission, give rise to the adult, tree-like colony.

The Zoothamnium colony is thus *dimorphic*, bearing individuals of two kinds: *nutritive zooids*, which feed and add to the colony by fission but are unable to give rise to a new colony, and *reproductive zooids*, which do not feed while attached, but are capable, after a period of free existence, of developing a mouth and stalk, and finally producing a new colony. Dimorphism is a differentiation of the individuals of a colony, just as the formation of axial fibre, gullet, contractile vacuole, and cilia are cases of differentiation of the protoplasm of a single cell.

LESSON XIII

SPECIES AND THEIR ORIGIN: THE PRINCIPLES OF CLASSIFICATION

More than once in the course of the foregoing lessons we have had occasion to use the word *species*—for instance, in Lesson I. (p. 8) it was stated that there were different kinds or species of Amœbæ, distinguished by the characters of their pseudopods, the structure of their nuclei, &c.

We must now consider a little more in detail what we mean by a species, and, as in all matters of this sort, the study of concrete examples is the best aid to the formation of clear conceptions, we will take, by way of illustration, some of the various species of Zoothamnium.

The kind described in the previous lesson is called *Zoothamnium arbuscula*. As Fig. 26, A, shows, it consists of a tolerably stout main stem, from the distal end of which spring a number of slender branches diverging in a brush-like manner, and bearing on short secondary branchlets the separate individuals of the colony: these are of two kinds, bell-shaped nutritive zooids, and globular reproductive zooids, so that the colony is dimorphic.

Zoothamnium (or, for the sake of brevity, *Z.*) *alternans* Fig. 27, A) is found also in sea-water, and differs markedly

from Z. arbuscula in the general form of the colony. The main stem is continued to the extreme distal end of the colony and terminates in a zooid; from it branches are given off right and left, and on these the remaining zooids are borne. To use Mr. Saville Kent's comparison, Z. arbus-

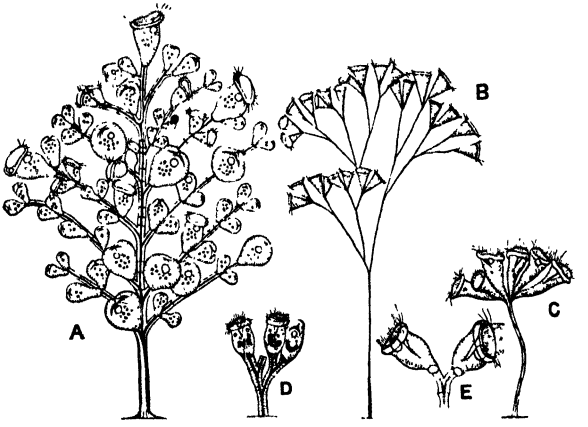

FIG. 27.—Species of Zoothamnium. A, *Z. alternans*. B, *Z. dichotomum*. C, *Z. simplex*. D, *Z. affine*. E, *Z. nutans*. (After Saville Kent.)

cula may be compared to a standard fruit tree, Z. alternans to an espalier. In this species also the colony is dimorphic.

Z. dichotomum (Fig. 27, B) is also dimorphic and presents a third mode of branching. The main stem divides into two, and each of the secondary branches does the same, so that a repeatedly forking stem is produced. The branching of this species is said to be *dichotomous*, while that of Z. alternans is *monopodial*, and that of Z. arbuscula *umbellate*.

Another mode of aggregation of the zooids is found in *Z. simplex* (Fig. 27, C), in which the stem is unbranched and

bears at its distal end about six zooids in a cluster. The zooids are more elongated than in any of the preceding species, and there are no special reproductive individuals, so that the colony is *homomorphic*.

In *Z. affine* (Fig. 27, D) the stalk is dichotomous but is proportionally thicker than in the preceding species, and bears about four zooids, all alike. It is found in fresh water attached to insects and other aquatic animals.

The last species we shall consider is *Z. nutans* (Fig. 27, E), which is the simplest known, never bearing more than two zooids, and sometimes only one.

A glance at Figs. 26 and 27 will show that these six species agree with one another in the general form of the zooids, in the characters of the nucleus, contractile vacuole, &c., in the arrangement of the cilia, and in the fact that they are all compound organisms, consisting of two or more zooids attached to a common stem, the axial fibre of which branches with it, *i.e.*, is continuous throughout the colony.

On account of their possessing these important characters in common, the species described are placed in the single *genus* Zoothamnium, and the characters summarized in the preceding paragraph are called *generic characters*. On the other hand the points of difference between the various species, such as the forking of the stem in *Z.* dichotomum, the presence of only two zooids in Z. nutans, and so on, are called *specific characters*. Similarly the name *Zoothamnium*, which is common to all the species, is the *generic name*, while those which are applied only to a particular species, such as *arbuscula*, *simplex*, &c., are the *specific names*. As was mentioned in the first lesson (p. 8), this method of naming organisms is known as the Linnean system of binomial nomenclature.

It will be seen from the foregoing account that by a

species we understand an assemblage of individual organisms, whether simple or compound, which agree with one another in all but unessential points, such as the precise number of zooids in Zoothamnium, which may vary considerably in the same species, and come, therefore, within the limits of *individual variation*. Similarly, what we mean by a genus is a group of species agreeing with one another in the broad features of their organization, but differing in detail, the differences being constant.

A comparison of the six species described brings out several interesting relations between them. For instance, it is clear that Z. arbuscula and Z. alternans are far more complex, *i.e.*, exhibit greater differentiation of the entire colony, than Z. simplex, or Z. nutans; so that, within the limits of the one genus, we have comparatively low or generalized, and comparatively high or specialized species. Nevertheless, a little consideration will show that we cannot arrange the species in a single series, beginning with the lowest and ending with the highest, for, although we should have no hesitation in placing Z. nutans at the bottom of such a list, it would be impossible to say whether Z. affine was higher or lower than Z. simplex, or Z. arbuscula than Z. alternans.

It is, however, easy to arrange the species into groups according to some definite system. For instance, if we take the mode of branching as a criterion, Z. nutans, affine, and dichotomum will all be placed together as being dichotomous, and Z. simplex and arbuscula as being umbellate—the zooids of the one and the branches of the other all springing together from the top of the main stem: on this system Z. alternans will stand alone on account of its monopodial branching. Or, we may make two groups, one of dimorphic forms, including Z. arbuscula, alternans, and

dichotomum, and another of homomorphic species, including Z. affine, simplex, and nutans. We have thus two very obvious ways of arranging or *classifying* the species of Zoothamnium, and the question arises—which of these, if either, is the right one? Is there any standard by which we can judge of the accuracy of a given classification of these or any other organisms, or does the whole thing depend upon the fancy of the classifier, like the arrangement of books in a library? In other words, are all possible classifications of living things more or less artificial, or is there such a thing as a *natural classification?*

Suppose we were to try and classify all the members of a given family—parents and grandparents, uncles and aunts, cousins, second cousins, and so on. Obviously there are a hundred ways in which it would be possible to arrange them—into dark and fair, tall and short, curly-haired and straight-haired and so on. But is is equally obvious that all these methods would be purely artificial, and that the only natural way, *i.e.*, the only way to show the real connection of the various members of the family with one another would be to classify them according to blood-relationship, in other words to let our classification take the form of a genealogical tree.

It may be said—what has this to do with the point under discussion, the classification of the species of Zoothamnium?

There are two theories which attempt to account for the existence of the innumerable species of living things which inhabit our earth: the theory of *creation* and the theory of *evolution*.

According to the theory of creation, all the individuals of every species existing at the present day—the tens of thousands of dogs, oak trees, amœbæ, and what not—are derived by a natural process of descent from a single indi-

vidual, or from a pair of individuals—in each case precisely resembling, in all essential respects, their existing descendants—which came into existence by a process outside the ordinary course of nature and known as Creation. On this hypothesis the history of the genus Zoothamnium would be represented by the diagram (Fig. 28); each of the species being derived from a single individual which came into

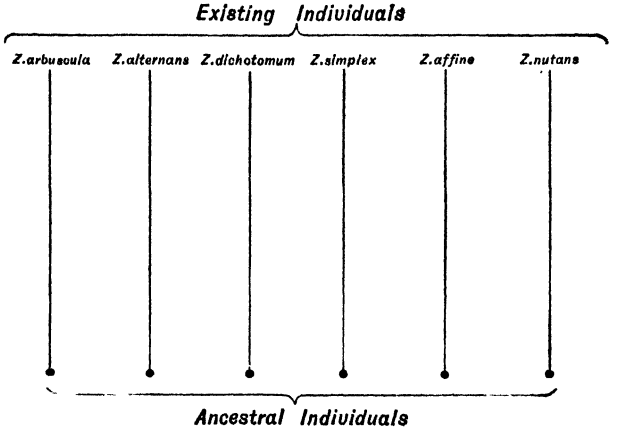

FIG. 28.—Diagram illustrating the origin of the species of Zoothamnium by creation.

existence, independently of the progenitors of all the other species, at some distant period of the earth's history.

Notice that on this theory the various species are no more actually *related* to one another than is either of them to Vorticella, or for the matter of that to Homo. The individuals of any one species are truly related since they all share a common descent, but there is no more relationship between the individuals of any two independently created species than between any two independently manufactured

chairs or tables. The words affinity, relationship, &c., as applied to different species are, on the theory of creation, purely metaphorical, and mean nothing more than that a certain likeness or community of structure exists; just as we might say that an easy chair was more nearly related to a kitchen chair than either of them to a three-legged stool.

We see therefore that on the hypothesis of creation the varying degrees of likeness and unlikeness between the species receive no explanation, and that we get no absolute criterion of classification: we may arrange our organisms, as nearly as our knowledge allows, according to their resemblances and differences, but the relative importance of the characters relied on becomes a purely subjective matter.

According to the rival theory—that of Descent or Organic Evolution—every species existing at the present day is derived by a natural process of descent from some other species which lived at a former period of the world's history. If we could trace back from generation to generation the individuals of any existing species we should, on this hypothesis, find their characters gradually change, until finally a period was reached at which the differences were so considerable as to necessitate the placing of the ancestral forms in a different species from their descendants at the present day. And in the same way if we could trace back the species of any one genus, we should find them gradually approach one another in structure until they finally converged in a single species, differing from those now existing but standing to all in a true parental relation.

Let us illustrate this by reference to Zoothamnium. As a matter of fact we know nothing of the history of the genus, but the comprehension of what is meant by the evolution of species will be greatly facilitated by framing a working hypothesis.

Suppose that at some distant period of the world's history

there existed a Vorticella-like organism which we will call A (Fig. 29), having the general characters of a single, stalked zooid of Zoothamnium (compare Fig. 26, F²), and suppose that, of the numerous descendants of this form, represented by the lines diverging from A, there were some in which both the zooids formed by the longitudinal division of the body remained attached to the stalk instead of one of them swimming off as in Vorticella. The result—it matters

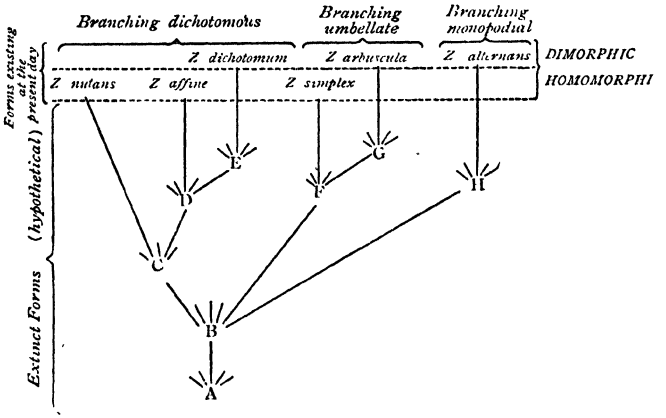

FIG. 29.—Diagram illustrating the origin of the species of Zoothamnium by evolution.

not for our present purpose how it may have been caused—would be a simple colonial organism consisting of two zooids attached to the end of a single undivided stalk. Let us call this form B.

Next let us imagine that in some of the descendants of B, represented as before by the diverging lines, the plane of division was continued downwards so as to include the distal end of the stalk: this would result in the production

of a form (C) consisting of two zooids borne on a forked stem and resembling Z. nutans. If, in some of the descendants of C, this process were repeated, each of the two zooids again dividing into two fixed individuals and the division as before affecting the stem, we should get a species (D) consisting of four zooids on a dichotomous stem, like Z. affine. Let the same process continue from generation to generation, the colony becoming more and more complex; we should finally arrive at a species E, consisting of numerous zooids on a complicated dichotomously branching stem, and therefore resembling Z. dichotomum.

Let us further suppose that, in some of the descendants of our hypothetical form B, repeated binary fission took place without affecting the stem: the result would be a new form F, consisting of numerous zooids springing in a cluster from the end of the undivided stem, after the manner of Z. simplex. From this a more complicated umbellate form (G), like Z. arbuscula, may be supposed to have originated, and again starting from B with a different mode of branching a monopodial form (H) might have arisen.

Finally, let it be assumed that while some of the descendants of the forms C, D, and F became modified into more and more complex species, others survived to the present time with comparatively little change, forming the existing species nutans, affine, and simplex: and that, in the similarly surviving representatives of E, G, and H, a differentiation of the individual zooids took place resulting in the evolution of the dimorphic species dichotomum, arbuscula, and alternans.

It will be seen that, on this hypothesis, the relative likeness and unlikeness of the species of Zoothamnium are explained as the result of their descent with greater or less modification or *divergence of character* from the ancestral form A: and that we get an arrangement or classification

in the form of a genealogical tree, which, on the hypothesis, is a strictly natural one, since it shows accurately the relationship of the various species to one another and to the parent stock. So that, on the theory of evolution, a natural classification of any given group of allied organisms is simply a genealogical tree, or, as it is usually called, a *phylogeny*.

It must not be forgotten that the forms A, B, C, D, E, F, G, and H are purely hypothetical: their existence has been assumed in order to illustrate the doctrine of descent by a concrete example. The only way in which we could be perfectly sure of an absolutely natural classification of the species of Zoothamnium would be by obtaining specimens as far back as the distant period when the genus first came into existence; and this is out of the question, since minute soft-bodied organisms like these have no chance of being preserved in the fossil state.

It will be seen that the theory of evolution has the advantage over that of creation of offering a reasonable explanation of certain facts. First of all the varying degrees of likeness and unlikeness of the species are explained by their having branched off from one another at various periods: for instance, the greater similarity of structure between Z. affine and Z. dichotomum than between either of them and any other species is due to these two species having a common ancestor in D, whereas to connect either of them, say with Z. arbuscula, we have to go back to B. Then again the fact that all the species, however complex in their fully developed state, begin life as a simple zooid which by repeated branching gradually attains the adult complexity, is a result of the repetition by each organism, in the course of its single life, of the series of changes passed through by its ancestors in the course of ages. In other words *ontogeny*,

or the evolution of the individual, is, in its main features, a recapitulation of *phylogeny* or the evolution of the race.

One other matter must be referred to in concluding the present lesson. It is obvious that the evolution of one species from another presupposes the occurrence of variations in the ancestral form. As a matter of fact such *individual variation* is of universal occurrence : it is a matter of common observation that no two leaves, shells, or human beings are precisely alike, and in our type genus Zoothamnium the number of zooids, their precise arrangement, the details of branching, &c., are all variables. This may be expressed by saying that *heredity*, according to which the offspring tends to resemble the parent in essentials, is modified by *variability*, according to which the offspring tends to differ from the parent in details. If from any cause an individual variation is perpetuated there is produced what is known as a *variety* of the species, and, according to the theory of the origin of species by evolution, such a variety may in course of time become a new species. Thus a variety is an incipient species, and a species is a (relatively) permanent variety.

It does not come within the scope of the present work to discuss either the causes of variability or those which determine the elevation of a variety to the rank of a species : both questions are far too complex to be adequately treated except at considerable length, and anything of the nature of a brief abstract could only be misleading. As a preliminary to the study of Darwin's *Origin of Species*, the student is recommended to read Romanes's *Evidences of Organic Evolution*, in which the doctrine of Descent is expounded as briefly as is consistent with clearness and accuracy.

LESSON XIV

FORAMINIFERA, RADIOLARIA, AND DIATOMS

In the four previous lessons we have learnt how a unicellular organism may attain very considerable complexity by a process of differentiation of its protoplasm. In the present lesson we shall consider briefly certain forms of life in which, while the protoplasm of the unicellular body undergoes comparatively little differentiation, an extraordinary variety and complexity of form is produced by the development of a *skeleton*, either in the shape of a hardened cell-wall or by the formation of hard parts within the protoplasm itself.

The name *Foraminifera* is given to an extensive group of organisms which are very common in the sea, some living near the surface, others at various depths. They vary in size from a sand-grain to a shilling. They consist of variously shaped masses of protoplasm, containing nuclei, and produced into numerous pseudopods, which are extremely long and delicate, and frequently unite with one another to form networks, as at × in Fig. 30. The cell-body of these organisms is therefore very simple, and may be compared to that of a multinucleate Amœba with fine radiating pseudopods.

But what gives the Foraminifera their special character is the fact that around the protoplasm is developed a cell-wall, sometimes membranous, but usually impregnated with calcium carbonate, and so forming a *shell*. In some cases, as in the genus *Rotalia* (Fig. 30), this is perforated by numerous small holes, through which the pseudopods are protruded, in others it has only one large aperture (Fig. 31),

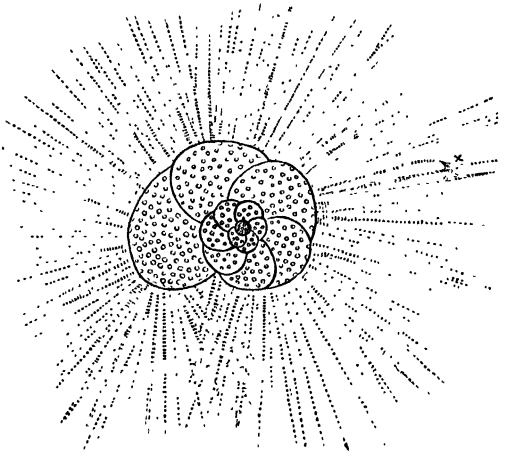

FIG. 30.—A living Foraminifer (*Rotalia*), showing the fine radiating pseudopods passing through apertures in the chambered shell: at × several of them have united. (From Gegenbaur.)

through which the protoplasm protrudes, sending off its pseudopods and sometimes flowing over and covering the outer surface of the shell. Thus while in some cases the shell has just the relations of a cell-wall with one or more holes in it, in others it becomes an internal structure, being covered externally as well as filled internally by protoplasm.

The mode of growth of Foraminifera is largely determined by the hard and non-distensible character of the cell-wall,

which when once formed is incapable of being enlarged. In the young condition they consist of a simple mass of protoplasm covered by a more or less globular shell, having at least one aperture. But in most cases as the cell-body grows, it protrudes through the aperture of the shell as a mass of protoplasm, at first naked, but soon becoming covered by the secretion around it of a second compartment or chamber of the shell. The latter now consists of two

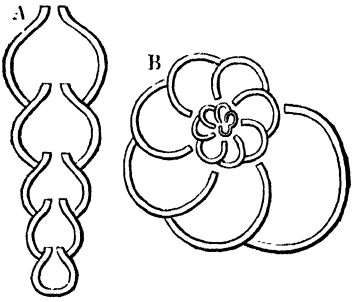

FIG. 31.—A, diagram of a Foraminifer in which new chambers are added in a straight line: the smallest first-formed chamber is below, the newest and largest is above and communicates with the exterior.
B, diagram of a Foraminifer in which the chambers are added in a flat spiral: the oldest and smallest chamber is in the centre, the newest and largest as before communicates with the exterior. (After Carpenter.)

chambers communicating with one another by a small aperture, and one of them—the last formed—communicating with the exterior. This process may go on almost indefinitely, the successive chambers always remaining in communication by small apertures through which continuity of the protoplasm is maintained, while the last formed chamber has a terminal aperture placing its protoplasm in free communication with the outer world.

The new chambers may be added in a straight line (Fig. 31, A) or in a gentle curve, or in a flat spiral (Fig. 31, B), or like the segments of a Nautilus shell, or more or less irregularly. In this way shells of great variety and beauty

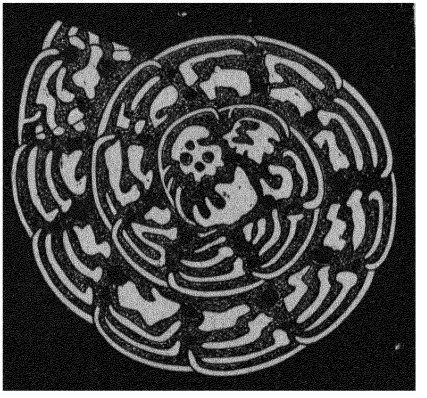

FIG. 32.—Section of one of the more complicated Foraminifera (*Alveolina*), showing the numerous chambers containing protoplasm (dotted), separated by partitions of the shell (white). × 60. (From Gegenbaur after Carpenter.)

of form are produced, often resembling the shells of Mollusca, and sometimes attaining a marvellous degree of complexity (Fig. 32). The student should make a point of examining mounted slides of some of the principal genera and of consulting the plates in Carpenter's *Introduction to the Study of Foraminifera* (Ray Society, 1862), or in Brady's *Report on the Foraminifera of the "Challenger" Expedition*, in order to get some notion of the great amount of differentiation attained by the shells of these extremely simple organisms.

The *Radiolaria* form another group of marine animalcules, the numerous genera of which are, like the Foraminifera, amongst the most beautiful of microscopic objects. They also (Fig. 33) consist of a mass of protoplasm giving off numerous delicate pseudopods (*psd*) which usually have a radial direction and sometimes unite to form networks. In the centre of the protoplasmic cell-body one or more nuclei (*nu*) of unusual size and complex structure are found.

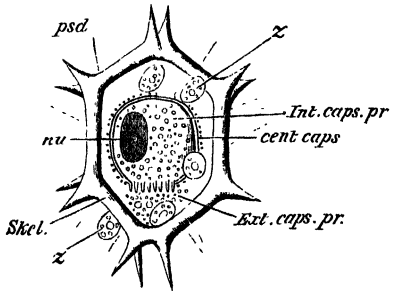

FIG. 33.—*Lithocircus annularis*, one of the Radiolaria, showing central capsule (*cent. caps.*), intra- and extra capsular protoplasm (*int. caps. pr.*, *ext. caps. pr.*), nucleus (*nu*), pseudopods (*psd*), silicious skeleton (*skel*), and symbiotic cells of Zooxanthella (*z*). (After Bütschli.)

In the interior of the protoplasm, surrounding the nucleus, is a sort of shell, called the *central capsule* (*cent. caps.*), formed of a membranous material, and perforated by pores which place the inclosed or *intra-capsular* protoplasm (*int. caps. pr.*) in communication with the surrounding or *extra-capsular* protoplasm (*ext. caps. pr.*). But besides this simple membranous shell there is often developed, mainly in the extra-capsular protoplasm, a skeleton (*skel*) formed in the majority of cases of pure silica, and often of surpassing beauty and complexity. One very exquisite form is shown

in Fig. 34 : it consists of three perforated concentric spheres connected by radiating spicules . the material of which it is composed resembles the clearest glass.

The student should examine mounted slides of the silicious shells of these organisms—sold under the name of *Polycystineæ*—and should consult the plates of Haeckel's *Die Radiolarien*: he cannot fail to be struck with the complexity

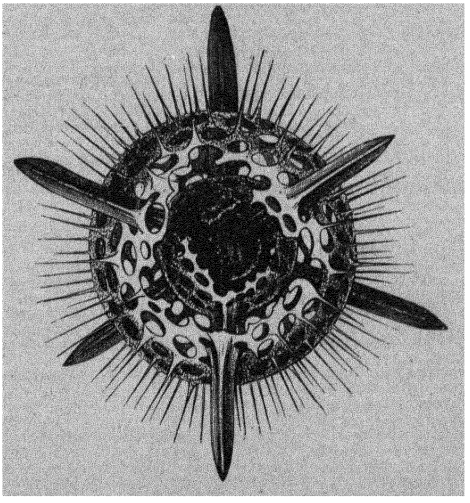

FIG. 34.—Skeleton of a Radiolarian (*Actinomma*), consisting of three concentric perforated spheres the two outer partly broken away to show the inner—connected by radiating spicules. (From Gegenbaur, after Haeckel.)

and variety attained by the skeletons of organisms which are themselves little more complex than Amœbæ.

Before leaving the Radiolaria, we must touch upon a matter of considerable interest connected with the physiology of the group. Imbedded usually in the extra-capsular

protoplasm are found certain little rounded bodies of a yellow colour, often known as "yellow cells" (Fig. 33, *z*). Each consists of protoplasm surrounded by a cell-wall of cellulose, and coloured by chlorophyll, with which is associated a yellow pigment of similar character called *diatomin*.

For a long time these bodies were a complete puzzle to biologists, but it has now been conclusively proved that they are independent organisms resembling the resting condition of Hæmatococcus, and called *Zooxanthella nutricola*.

Thus an ordinary Radiolarian, such as Lithocircus (Fig. 33), consists of two quite distinct things, the Lithocircus in the strict sense of the word *plus* large numbers of Zooxanthellæ associated with it. The two organisms multiply quite independently of one another: indeed Zooxanthella has been observed to multiply by fission after the death of the associated Radiolarian.

This living together of two organisms is known as *symbiosis*. It differs essentially from parasitism (see p. 123), in which one organism preys upon another, the host deriving no benefit but only harm from the presence of the parasite. In symbiosis, on the contrary, the two organisms are in a condition of mutually beneficial partnership. The carbon dioxide and nitrogenous waste given off by the Radiolarian serve as a constant food-supply to the Zooxanthella: at the same time the latter by decomposing the carbon dioxide provides the Radiolarian with a constant supply of oxygen, and at the same time with two important food-stuffs—starch and proteids—which, after solution, diffuse from the protoplasm of the Zooxanthella into that of the Radiolarian. The Radiolarian may therefore be said to keep the Zooxanthellæ constantly manured, while the Zooxanthellæ in return supply the Radiolarian with abundance of oxygen and of ready-digested food. It is as if a Hæmatococcus ingested by an

Amœba retained its vitality instead of being digested: it would under these circumstances make use of the carbon dioxide and nitrogenous waste formed as products of katabolism by the Amœba, at the same time giving off oxygen and forming starch and proteids. The oxygen evolved would give an additional supply of this necessary gas to the Amœba, and the starch after conversion into sugar and the proteids after being rendered diffusible would in part diffuse through the cell-wall of the Hæmatococcus into the surrounding protoplasm of the Amœba, to which they would be a valuable food.

Thus, as it has been said, the relation between a Radiolarian and its associated yellow-cells are precisely those which obtain between the animal and vegetable kingdoms generally.

The *Diatomaceæ* or *Diatoms*, as they are often called for the sake of brevity, are a group of minute organisms, included under a very large number of genera and species, and so common that there is hardly a pond or stream in which they do not occur in millions

Diatoms vary almost indefinitely in form: they may be rod-shaped, triangular, circular, and so on. Their essential structure is, however, very uniform: the cell-body contains a nucleus (Fig. 35, A, *nu*) and vacuoles (*vac*), as well as two large chromatophores (*chr*) of a brown or yellow colour; these are found to contain chlorophyll, the characteristic green tint of which is veiled, as in Zooxanthella, by diatomin. The cell is motile, executing curious, slow, jerky or gliding movements caused by the protrusion of delicate threads of mucilage from between the valves of the cell-wall: the threads are shot out at intervals in a given direction, and, by the resistance of the water, the diatom is jerked in the opposite direction.

The most interesting feature in the organisation of diatoms is however the structure of the cell-wall: it consists of two parts or *valves* (B, C, *c. w*, *c. w'*), each provided with a rim or

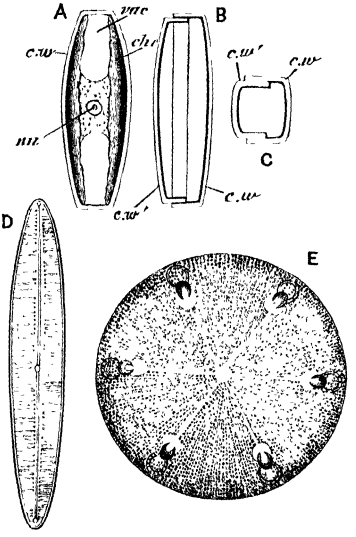

FIG. 35.—A, semi-diagrammatic view of a diatom from its flat face, showing cell-wall (*c. w*) and protoplasm with nucleus (*nu*), two vacuoles (*vac*), and two chromatophores (*chr*).

B, diagram of the shell of a diatom from the side, *i.e.*, turned on its long axis at right angles to A, showing the two valves (*c. w*, *c. w'*) with their overlapping girdles.

C, the same in transverse section.

D, surface view of the silicious shell of *Navicula truncata*.

E, surface view of the silicious shell of *Aulacodiscus sollittianus*.

(D, after Donkin; E, after Norman.)

girdle, and so disposed that in the entire cell the girdle of one valve (*c. w*) fits over that of the other (*c. w'*) like the lid of a pill-box. The cell-wall is impregnated with silica, so that diatoms can be boiled in strong acid or exposed to

cell, the *ovum*[1] or egg-cell (D[4], *ov*), which, by the gelatinization and subsequent disappearance of a portion of the wall of the ovary, is in free contact with the surrounding water.

At the same time the protoplasm of the spermary undergoes multiple fission, becoming converted into numerous minute green bodies (D[5]), each with two flagella, called *sperms*.[2] These are liberated by the rupture of the spermary (D[7]) at its distal end, and swim freely in the water.

Some of the sperms make their way to an ovary, and, as it has been expressed, seem to grope about for the aperture, which they finally pass through (D[6]), and are then seen moving actively in the space between the aperture and the colourless distal end of the ovum. One of them, and probably only one, then attaches itself to the ovum and becomes completely united with it, forming the *oosperm*,[3] a body which we must carefully distinguish from the ovum, since, while agreeing with the latter in form and size, it differs in having incorporated with it the substance of a sperm.

Almost immediately the oosperm (D[7], *osp*) surrounds itself with a cellulose wall, and numerous oil-globules are formed in its interior. It becomes detached from the ovary, and, after a period of rest, germinates (E[1], E[2]) and forms a new Vaucheria plant.

It is obvious that the fusion of the sperm with the ovum is a process of conjugation in which the conjugating bodies differ strikingly in form and size, one—the *megagamete* or ovum—being large, stationary, and more or less amœboid: the other—the *microgamete* or sperm—small, active, and

[1] Frequently called *oosphere*.

[2] Often called *spermatozooids* or *antherozooids*.

[3] Often called *oospore*.

flagellate. In other words, we have a more obvious case of sexual differentiation than was found to occur in Vorticella, (p. 132): the large inactive egg-cell which furnishes by far the greater portion of the material of the oosperm is the female gamete; the small active sperm-cell, the function of which is probably (see Lesson XXIII) to furnish additional nuclear material, is the male gamete.

Similarly the oosperm is evidently a zygote, but a zygote formed by the union of the highly differentiated gametes, ovum and sperm, just as a zygospore (p. 166) is one formed by the union of equal sized gametes.

As we shall see, this form of conjugation—often distinguished as *fertilization*—occurs in a large proportion of flowerless plants, such as mosses and ferns (Lessons XXX. and XXXI.), as well as in all animals but the very lowest. From lowly water-weeds up to ferns and club mosses, and from sponges and polypes up to man, the process of sexual reproduction is essentially the same, consisting in the conjugation of a microgamete or sperm with a megagamete or ovum; a zygote, the oosperm or unicellular embryo, being produced, which afterwards develops into an independent plant or animal of the new generation. It is a truly remarkable circumstance that what we may consider as the highest form of the sexual process should make its appearance so low down in the scale of life.

The nutrition of Vaucheria is purely holophytic; its food consists of a watery solution of mineral salts and of carbon dioxide, the latter being split up, by the action of the chromatophores, into carbon and oxygen.

Mucor and Vaucheria are examples of non-cellular plants which attain some complexity by elongation and branching.

The maximum differentiation attainable in this way by a non-cellular plant may be illustrated by a brief description of a sea-weed belonging to the genus *Caulerpa*.

Caulerpa (Fig. 39) is commonly found in rock-pools between tide-marks, and has the form of a creeping stem from which root-like fibres are given off downwards and branched leaf-like organs upwards. These "leaves" may attain a length of 30 cm. (1 ft.) or more. So that, on a

FIG. 39.—*Caulerpa scalpelliformis* (⅔ nat. size), showing the stem-like, root-like, and leaf-like portions of the non-cellular plant. (After Harvey.)

superficial examination, Caulerpa appears to be as complex an organism as a moss (compare Fig. 39 with Fig. 108, A). But microscopical examination shows that the plant consists of a single continuous mass of vacuolated protoplasm, containing numerous nuclei and green chromatophores and covered by a continuous cell-wall. Large and complicated in form as it is, the whole plant is therefore nothing more than a continuous mass of protoplasm exhibiting no cellular structure.

LESSON XVII

THE DISTINCTIVE CHARACTERS OF ANIMALS AND PLANTS

HITHERTO the words "animal" and "plant" have been either avoided altogether or used incidentally without any attempt at definition. We are now however in a position to consider in some detail the precise meaning of the two words, since in the last half-dozen lessons we have been dealing with several organisms which can be assigned without hesitation to one or other of the two great groups of living things. No one would dream of calling Paramœcium and Stylonychia plants, or Mucor and Vaucheria animals, and we may therefore use these forms as a starting-point in an attempt to form a clear conception of what the names *plant* and *animal* really signify, and how far it is possible to place the lowly organisms described in the earlier lessons in either the vegetable or the animal kingdom.

Let us consider, first of all, the chief points of resemblance and of difference between the indubitable animal Paramœcium on the one hand, and the two indubitable plants Mucor and Vaucheria on the other.

In the first place, the essential constituents of all three organisms is protoplasm, in which are contained one or more nuclei. But in Paramœcium the protoplasm is invested

only by a delicate cuticle interrupted at the mouth and anus, while in Mucor and Vaucheria the outer layer is formed by a firm, continuous covering of cellulose.

We thus have as the first morphological difference between our selected animal and vegetable organisms the absence of a cellulose cell-wall in the former and its presence in the latter. This is a fundamental distinction, and applies equally well to the higher forms. The constituent cells of plants are in nearly all cases covered with a cellulose coat (p. 60), while there is no case among the higher animals of cells being so invested.

Next, let us take a physiological character. In all three organisms there is constant waste of substance which has to be made good by the conversion of food material into protoplasm : in other words, constructive and destructive metabolism are continually being carried on. But when we come to the nature of the food and the mode of its reception, we meet at once with a very fundamental difference. In Paramœcium the food consists of living organisms taken whole into the interior of the body, and the digestion of this solid proteinaceous food is the necessary prelude to constructive metabolism. In Vaucheria the food consists of a watery solution of carbon dioxide and mineral salts—*i.e.*, it is liquid and inorganic, its nitrogen being in the form of nitrates or of simple ammonia compounds. Mucor, like Paramœcium, contains no chlorophyll, and is therefore unable to use carbon dioxide as a food : like Vaucheria, it is prevented by its continuous cellulose investment from ingesting solid food, and is dependent upon an aqueous solution. It takes its carbon in the form of sugar or some such compound, while it can make use of nitrogen either in the simple form of a nitrate or an ammonia salt, or in the complex form of proteids or peptones.

In this case also our selected organisms agree with animals and plants generally. Animals, with the exception of some internal parasites, ingest solid food, and they must all have their nitrogen supplied in the form of proteids, being unable to build up their protoplasm from simpler compounds. Plants take their food in the form of a watery solution; those which possess chlorophyll take their carbon in the form of carbon dioxide and their nitrogen in that of a nitrate or ammonia salt: those devoid of chlorophyll cannot, except in the case of some Bacteria, make use of carbon dioxide as a food, and are able to obtain nitrogen either from simple salts or from proteids. Chlorophyll-less plants are therefore nourished partly like green plants, partly like animals.

This difference in the character of the food is connected with a morphological difference. Animals have, as a rule, an ingestive aperture or mouth, and some kind of digestive cavity, either permanent (stomach) or temporary (food-vacuole). In plants neither of these structures exists.

Another difference which was referred to at length in an early lesson (p. 32), is not strictly one between plants and animals, but between organisms with and organisms without chlorophyll. It is that in green plants the nutritive processes result in deoxidation, more oxygen being given out than is taken in; while in animals and not-green plants the precise contrary is the case.

There is also a difference in the method of excretion. In Paramœcium there is a special structure, the contractile vacuole, which collects the superfluous water taken in with the food and expels it, doubtless along with nitrogenous and other waste matters. In Vaucheria and Mucor there is no contractile vacuole, and excretion is simply performed by

diffusion from the general surface of the organism into the surrounding medium.

This character also is of some general importance. The large majority of animals possess a special organ of excretion, plants have nothing of the kind.

Another difference has to do with the general form of the organism. Paramœcium has a certain definite and constant shape, and when once formed produces no new parts. Vaucheria and Mucor are constantly forming new branches, so that their shape is always changing and their growth can never be said to be complete.

Finally, we have what is perhaps the most obvious and striking distinction of all. Paramœcium possesses in a conspicuous degree the power of automatic movement; in both Mucor and Vaucheria the organism, as a whole, exhibits no automatism but only the slow movements of growth. The spores and sperms of Vaucheria are, however, actively motile.

Thus, taking Paramœcium as a type of animals, and Mucor and Vaucheria as types of plants, we may frame the following definitions:—

Animals are organisms of fixed and definite form, in which the cell-body is not covered with a cellulose wall. They ingest solid proteinaceous food, their nutritive processes result in oxidation, they have a definite organ of excretion, and are capable of automatic movement.

Plants are organisms of constantly varying form in which the cell-body is surrounded by a cellulose wall; they cannot ingest solid food, but are nourished by a watery solution of nutrient materials. If chlorophyll is present the carbon dioxide of the air serves as a source of carbon, nitrogen is obtained from simple salts, and the nutritive processes

result in deoxidation; if chlorophyll is absent carbon is obtained from sugar or some similar compound, nitrogen either from simple salts or from proteids, and the process of nutrition is one of oxidation. There is no special excretory organ, and, except in the case of certain reproductive bodies, there is usually no locomotion.

Let us now apply these definitions to the simple forms described in the first eight lessons, and see how far they will help us in placing those organisms in one or other of the two "kingdoms" into which living things are divided.

Amœba has a cell-wall, probably nitrogenous, in the resting condition: it ingests solid proteids, its nutrition being therefore holozoic: it has a contractile vacuole: and it performs amœboid movements. It may therefore be safely considered as an animal.

Hæmatococcus has a cellulose wall: it contains chlorophyll and its nutrition is purely holophytic: a contractile vacuole is present in H. lacustris: and its movements are ciliary.

Euglena has a cellulose wall in the encysted state: in virtue of its chlorophyll it is nourished by the absorption of carbon dioxide and mineral salts, but it can also ingest solid food through a special mouth and gullet: it has a contractile vacuole, and performs both euglenoid and ciliary movements.

In both these organisms we evidently have conflicting characters: the cellulose wall and holophytic nutrition would place them both among plants, while from the contractile vacuole and active movements of both genera and from the holozoic nutrition of Euglena we should group them with animals. That the difficulty is by no means

easily overcome may be seen from the fact that both genera are claimed at the present day both by zoologists and by botanists. For instance, Prof. Huxley considered Hæmatococcus as a plant, and expressed doubts about Euglena: Mr. Saville Kent ranks Hæmatococcus as a plant and Euglena as an animal; Prof. Sachs and Mr. Thiselton Dyer place both genera in the vegetable kingdom; while Profs. Ray Lankester and Butschli group them both among animals.

In Heteromita the only cell-wall is the delicate cuticle, which in the zygote is firm enough to hold the spores up to the moment of their escape: food is taken exclusively by absorption, and nutrition is wholly saprophytic: there is a contractile vacuole, and the movements are ciliary.

Here again the characters are conflicting: the probable absence of cellulose, the contractile vacuole, and the cilia all have an "animal" look, but the mode of nutrition is that of a fungus.

In Protomyxa there is a decided preponderance of animal characteristics—ingestion of living prey, and both amœboid and ciliary movements. There is no chlorophyll, and the composition of the cell-wall is not known.

In the Mycetozoa, the life-history of which so closely resembles that of Protomyxa, the cyst in the resting stage consists of cellulose, and so does the cell-wall of the spore: nutrition is holozoic, a contractile vacuole is present in the flagellulæ, and both amœboid and ciliary movements are performed. Here again we have a puzzling combination of animal and vegetable characters, and as a consequence we find these organisms included among plants—under the name of *Myxomycetes* or "slime-fungi"—by Sachs and Goebel, while De Bary, Butschli, and Ray Lankester place them in the animal kingdom.

In Saccharomyces there is a clear preponderance of vegetable characters. The cell-wall consists of cellulose, nutrition takes place by absorption and proteids are not essential, there is no contractile vacuole, and no motile phase.

Lastly, in the Bacteria the cell-wall is composed of cellulose, nutrition is usually saprophytic, there is no contractile vacuole, and the movements are ciliary. So that in all the characters named, save in the presence of cellulose and the absence of a contractile vacuole, the Bacteria agree with Heteromita, yet they are universally—except by Prof. Claus—placed among plants, while Heteromita is as constantly included among animals.

We see then that while it is quite easy to divide the higher organisms into the two distinct groups of plants and animals, any such separation is by no means easy in the case of the lowest forms of life. It was in recognition of this fact that Haeckel proposed, many years ago, to institute a third "kingdom," called *Protista*, to include all unicellular organisms. Although open to many objections in practice, there is a great deal to be said for the proposal. From the strictly scientific point of view it is quite as justifiable to make three subdivisions of living things as two: the line between animals and plants is quite as arbitrary as that between protists and plants or between protists and animals, and no more so: the chief objection to the change is that it doubles the difficulties by making two artificial boundaries instead of one.

The important point for the student to recognise is that these boundaries *are* artificial, and that there are no scientific frontiers in Nature. As in the liquefaction of gases there is a "critical point" at which the substance under experiment is neither gaseous nor liquid: as in a mountainous country it is impossible to say where mountain ends and valley

LESSON XX

MONOSTROMA, ULVA, AND NITELLA

It was pointed out in a previous lesson (p. 193) that the highest and most complicated fungi, such as the mushrooms, are found on analysis to be built up of linear aggregates of cells—to consist of hyphæ so interwoven as to form structures often of considerable size and of definite and regular form.

This is not the case with the Algæ or lower green plants—a group to which Vaucheria, Caulerpa, Spirogyra, the sea-moss, and, in the view of some authors, Hæmatococcus and Euglena, belong. These agree with fungi in the fact that at the lowest among them (*e.g.* Zooxanthella) are unicellular, and others (*e.g.* Spirogyra) simple linear aggregates; but the higher forms, such as the majority of sea-weeds, have, as it were, gone beyond the fungi in point of structure and attained a distinctly higher stage of morphological differentiation. This will be made clear by a study of three typical genera.

Amongst the immense variety of sea-weeds found in rock-pools between high and low water-marks are several kinds having the form of flat irregular expansions or of bladder-

like masses, of a bright green colour and very transparent. One of these is the genus *Monostroma*, of which M. bullosum is a fresh-water species.

Examined microscopically the plant (Fig. 43) is found to consist of a single layer of close-set, green cells, the cell-walls of which are in close approximation, so that the cell-bodies appear as if embedded in a continuous layer of transparent cellulose. Thus Monostroma, like Spirogyra, is only one

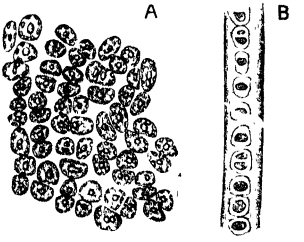

FIG. 43.—*Monostroma.*

A, surface view of M. bullosum, showing the cells embedded in a common layer of cellulose: many of them are in various stages of division.

B, vertical section of M. laceratum, showing the arrangement of the cells in a single layer.

(A after Reinke: B after Cooke.)

cell thick (B), but unlike that genus it is not one but many cells broad. In other words, instead of being a linear it is a *superficial aggregate.*

To use a geometrical analogy:—a unicellular organism like Hæmatococcus may be compared to a point; a linear aggregate like Penicillium or Spirogyra to a line; a superficial aggregate like Monostroma to a plane.

Growth takes place by the binary fission of the cells (A), but here again there is a marked and important difference from Spirogyra. In the latter the plane of division is always

at right angles to the long axis of the filament, so that growth takes place in one dimension of space only, namely in length. In Monostroma the plane of division may be inclined in any direction provided it is perpendicular to the surface of the plant, so that growth goes on in two dimensions of space, namely in length and breadth.

Another of the flat, leaf-like, green sea-weeds is the very common genus *Ulva*, sometimes called "sea-lettuce." It consists of irregular, more or less lobed expansions with crinkled edges, and under the microscope closely resembles Monostroma, with one important difference: it is formed not of one but of two layers of cells, and is therefore not a superficial but a *solid aggregate*. To return to the geometrical analogy used above it is to be compared not to a plane but to a solid body.

As in Monostroma growth takes place by the binary fission of the cells. But these divide not only along variously inclined planes at right angles to the surface of the plant but also along a plane parallel to the surface, so that growth takes place in all three dimensions of space—in length, breadth, and thickness.

Ulva may be looked upon as the simplest example of a solid aggregate, being built up of similar cells, and therefore exhibiting no *cell-differentiation*.

We shall now make a detailed study of a solid aggregate in which the constituent cells differ very considerably from one another in form and size, the result being a degree of complexity far beyond anything we have hitherto met with.

Nitella (Fig. 44, A) is a not uncommon fresh-water weed, found in ponds and water-races, and distinguished at once

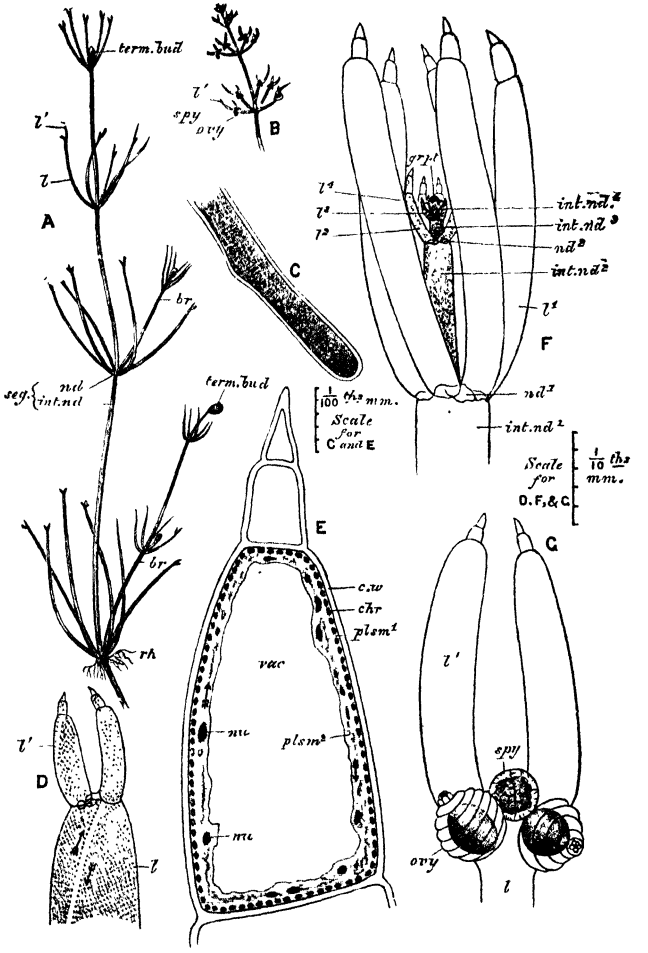

FIG. 44.—*Nitella*[1].

A, the entire plant (nat. size), showing the segmented stem, each seg-

[1] This and the following figures are taken from a New Zealand species closely allied to, if not identical with, the British *N. flexilis*.

ment (*seg*) consisting of a proximal internode (*int. nd*) and distal node (*nd*): the leaves (*l*) arranged in whorls and ending in leaflets (*l'*): the rhizoids (*rh*): and two branches (*br*), each springing from the axil of a leaf and ending, like the main stem, in a terminal bud (*term. bud*).

B, distal end of a shoot with gonads attached to the leaves: *ovy*, the ovaries; *spy*, the spermaries.

C, distal end of a rhizoid.

D, distal end of a leaf (*l*) with two leaflets (*l'*), showing the chromatophores and the white line. The arrows indicate the direction of rotation of the protoplasm.

E, distal end of a leaflet, showing the general structure of a typical cell of Nitella in optical section: *c. w*, the cell-wall; *plsm*^{1}, the quiescent outer layer of protoplasm containing chromatophores (*chr*); *plsm*^{2}, the inner layer, rotating in the direction indicated by the arrows, and containing nuclei (*nu*); *vac*, the large vacuole.

F, terminal bud, partly dissected, showing the nodes (*nd*), internodes (*int. nd*), and leaf-whorls (*l*), numbered from 1 to 4, starting from the proximal end; *gr. pt*, growing point.

G, distal end of a leaf (*l*) with two leaflets (*l'*), at the base of which are attached a spermary (*spy*) and two ovaries (*ovy*).

from such low Algæ as Vaucheria and Spirogyra by its external resemblance to one of the higher plants, since it presents structures which may be distinguished as stem, branches, leaves, &c.

A Nitella plant consists of a slender cylindrical stem, some 15–20 cm. and upwards in length, but not more than about $\frac{1}{2}$ mm. in diameter. The proximal end is loosely rooted to the mud at the bottom of the stream or pond by delicate root-filaments or *rhizoids* (A, *rh*): the distal end is free. Springing from it at intervals are circlets or *whorls* of delicate, pointed *leaves* (*l*).

Owing to the regular arrangement of the leaves the stem is divisible into successive sections or *segments* (*seg*), each consisting of a very short distal division or *node* (*nd*) from which the leaves spring, and of an elongated proximal division or *internode* (*int. nd*), which bears no leaves.

Throughout the greater part of the stem the whorls of leaves are disposed at approximately equal distances from one another, so that the internodes are of equal length, but

towards the distal end the internodes become rapidly shorter and the whorls consequently closer together, until, at the actual distal end, a whorl is found the leaves of which, instead of spreading outwards like the rest, are curled upwards so that their points are in contact. In this way is formed the terminal bud (*term. bud*), by which the uninjured stem is always terminated distally.

The angle between the stem and a leaf, above (distal to) the attachment of the latter, is called the *axil* of the leaf. There is frequently found springing from the axil of one of the leaves in a whorl a *branch* or *shoot* (*br*) which repeats the structure of the main stem, *i.e.* consists of an axis from which spring whorls of leaves, the whole ending in a terminal bud. The axis or stem of a shoot is called a *secondary axis*, the main stem of the plant being the *primary axis*. It is important to notice that both primary and secondary axes always end in terminal buds, and thus differ from the leaves which have pointed extremities.

The rhizoids or root-filaments (*rh*) arise, like the leaves and branches, exclusively from nodes.

In the autumn the more distal leaves present a peculiar appearance, owing to the development on them of the *gonads* or sexual reproductive organs (Fig. 44, B and C): of these the *spermaries* (antheridia) look very like minute oranges, being globular structures (*spy*) of a bright orange colour: the *ovaries* (oogonia) are flask-shaped bodies (*ovy*) of a yellowish brown colour when immature, but turning black after the fertilization of the ova.

Examined under the microscope each internode is found to consist of a single gigantic cell (F, *int. nd*^{2}) often as much as 3 or 4 cm. long in the older parts of the plant. A node on the other hand is composed of a transverse plate of small

cells (*nd*[1]) separating the two adjacent internodes from one another. The leaves consist each of an elongated proximal cell like an internode (D, *l*; F, *l*[1]), then of a few small cells having the character of a node, and finally of two or three leaflets (D, G, *l'*), each consisting usually of three cells, the distal one of which is small and pointed.

Thus the Nitella plant is a solid aggregate in which the cells have a very definite and characteristic arrangement.

The details of structure of a single cell are readily made out by examining a leaflet under a high power. The cell is surrounded by a wall of cellulose (E, *c.w*) of considerable thickness. Within this is a layer of protoplasm (primordial utricle, p. 196), enclosing a large central vacuole (*vac*), and clearly divisible into two layers, an outer (*plsm*[1]) in immediate contact with the cell-wall, and an inner (*plsm*[2]) bounding the vacuole.

In the outer layer of protoplasm are the chromatophores or chlorophyll-corpuscles (*chr*) to which the green colour of the plant is due. They are ovoidal bodies, about $\frac{1}{100}$ mm. long, and arranged in obliquely longitudinal rows (D). On opposite sides of the cylindrical cell are two narrow oblique bands devoid of chromatophores and consequently colourless (D). The chromatophores contain minute starch grains.

The inner layer of protoplasm contains no chlorophyll corpuscles, but only irregular, colourless granules, many of which are nuclei (E, *nu*: see below, p. 211). If the temperature is not too low this layer is seen to be in active rotating movement, streaming up one side of the cell and down the other (E), the boundary between the upward and downward currents being marked by the colourless bands just mentioned, along which no movement takes place (D). This *rotation* of protoplasm is a form of contractility very

common in vegetable cells in which, owing to the confining cell-wall, no freer movement is possible.

The numerous nuclei (E, *nu*) are rod-like and often curved: they can be seen to advantage only after staining (Fig. 45). Lying as they do in the inner layer of protoplasm, they are carried round in the rotating stream.

In the general description of the plant it was mentioned that the stem ended distally in a terminal bud (Fig. 44, A, *term. bud*) formed of a whorl of leaves with their apices curved towards one another. If these leaves (F, l^1) are dissected away, the node from which they spring (nd^1) is found to give rise distally to a very short internode (*int.* nd^2), above which is a node (nd^2) giving rise to a whorl of very small leaves (l^2), also curved inwards so as to form a bud. Within these is found another segment consisting of a still smaller internode (*int.* nd^3) and node, bearing a whorl of extremely small leaves (l^3), and within these again a segment so small that its parts (*int.* nd^4, l^4) are visible only under the microscope. The minute blunt projections (l^4), which are the leaves of this whorl, surround a blunt, hemispherical projection (*gr. pt*), the actual distal extremity of the plant—the *growing point* or *punctum vegetationis*.

The structure of the growing point and the mode of growth of the whole plant is readily made out by examining vertical sections of the terminal bud in numerous specimens (Fig. 45).

The growing point is formed of a single cell, the apical cell (A, *ap. c*), approximately hemispherical in form and about $\frac{1}{20}$ mm. in diameter. Its cell-wall is thick, and its cell-body formed of dense granular protoplasm containing a large rounded nucleus (*nu*) but no vacuole.

In the living plant the apical cell is continually undergoing binary fission. It divides along a horizontal plane, *i.e.*, a

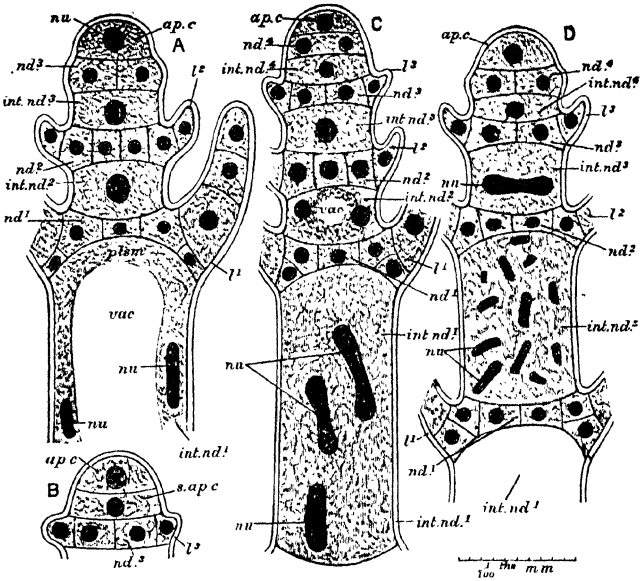

FIG. 45.—*Nitella*: Vertical sections of the growing point at four successive stages. The nodes (*nd*), internodes (*int. nd*), and leaf-whorls (*l*) are all numbered in order from the proximal to the distal end of the bud, the numbers corresponding in all the figures. The proximal segment (*int. nd*¹, *nd*¹, *l*¹) in these figures corresponds with the third segment (*int. nd*³, *l*³) shown in Fig. 44, F.

In A, the apical cell (*ap. c*) is succeeded by a very rudimentary node (*nd*³) without leaves: *int. nd*¹ is in vertical section, showing the protoplasm (*plsm*), vacuole (*vac*), and two nuclei (*nu*).

In B, the apical cell has divided transversely, forming a new apical cell (*ap. c*) and a sub-apical cell (*s. ap. c*): the leaves (*l*³) of *nd*³ have appeared.

In C, the sub-apical cell has divided transversely into the proximally-situated internode (*int. nd*⁴) and the distally-situated node (*nd*⁴) of a new segment; in the node the nucleus has divided preparatory to cell-division. The previously formed segments have increased in size: *int. nd*² has developed a vacuole (*vac*), and its nucleus has divided (comp. *int. nd*² in A): *int. nd*¹ is shown in surface view with three dividing nuclei (*nu*).

In D, *nd*⁴ has divided vertically, forming a transverse plate of cells, and is now as far advanced as *nd*³ in A: the nucleus of *int. nd*³ is in the act of dividing, while *int. nd*², shown in surface view, now contains numerous nuclei, some of them in the act of dividing.

plane parallel to its base, into two cells, the upper (distal) of which is the new apical cell (B, *ap. c*), while the lower is now distinguished as the *sub-apical* or *segmental cell* (*s. ap. c*). The sub-apical cell divides again horizontally, forming two cells, the uppermost of which (C, nd^4) almost immediately becomes divided by vertical planes into several cells (D, nd^4); the lower (C, D, *int.* nd^1) remains undivided.

The sub-apical cell is the rudiment of an entire segment; the uppermost of the two cells into which it divides is the rudiment of a node, the lower of an internode. The future fate of the two is shown at once by the node dividing into a horizontal plate of cells while the internode remains unicellular.

Soon the cells of the new node begin to send out short blunt processes arranged in a whorl: these increase in size, undergo division, and form leaves (A—D, l^2, l^3).

These processes are continually being repeated; the apical cell is constantly producing new sub-apical cells, the sub-apical cells dividing each into a nodal and an internodal cell; and the nodal cell dividing into a horizontal plate of cells and giving off leaves, while the internodal cell remains undivided.

The special characters of the fully-formed parts of the plant are due to the unequal growth of the new cells. The nodal cells soon cease to grow and undergo but little alteration (comp. nd^1 and nd^3), whereas the internodes increase immensely in length, being quite 3,000 times as long when full-grown as when first separated from the sub-apical cell. The leaves also, at first mere blunt projections (A, l^2), soon increase sufficiently in length to arch over the growing point and so form the characteristic terminal bud: gradually they open out and assume the normal position, their successors of the next younger whorl having in the meantime developed

sufficiently to take their place as protectors of the growing point.

The multinucleate condition of the adult internodes is also a result of gradual change. In its young condition an internodal cell has a single rounded nucleus (A, *int. nd*^{2}, *int. nd*^{3}), but by the time it is about as long as broad the nucleus has begun to divide (D, *int. nd*^{3}; C, *int. nd*^{2}), and when the length of the cell is equal to about twice its breadth, the nucleus has broken up into numerous fragments (C, *int. nd*^{1}, D, *int. nd*^{2}), many of them still in active (amitotic) division. This repeated fission of the nucleus reminds us of what was found to occur in Opalina (p. 123).

Thus the growth of Nitella like that of Penicillium (p. 190), is apical: new cells arise only in the terminal bud, and, after the first formation of nodes, internodes, and leaves, the only change undergone by these parts is an increase in size accompanied by a limited differentiation of character.

A shoot arises by one of the cells in a node sending off a projection distal to a leaf, *i.e.*, in an axil: the process separates from the parent cell and takes on the characters of the apical cell of the main stem, the structure of which is in this way exactly repeated by the shoot.

The leaves, unlike the branches, are strictly limited in growth. At a very early period the apical cell of a leaf becomes pointed and thick-walled (Fig. 44, E), and after this no increase in the number of cells takes place.

The rhizoids also arise exclusively from nodal cells: they consist of long filaments (Fig. 44, C), not unlike Mucor-hyphæ but occasionally divided by oblique septa into linear aggregates of cells, and increase in length by apical growth.

The structure of the gonads is peculiar and somewhat complicated.

As we have seen, the spermary (Fig. 44, G, *spy*) is a globular, orange coloured body attached to a leaf by a short stalk. Its wall is formed of eight pieces or *shields*, which fit against one another by toothed edges, so that the entire spermary may be compared to an orange in which an equatorial incision and two meridional incisions at right angles to one another have been made through the rind, dividing

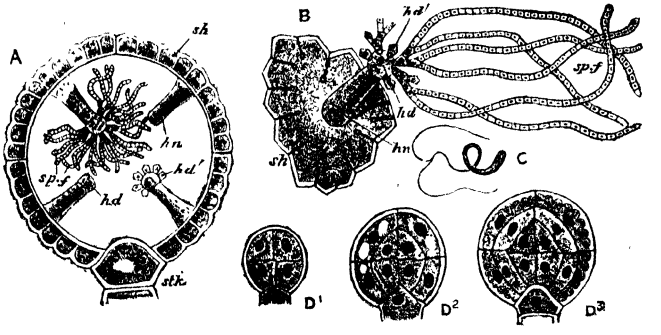

FIG. 46.—A, diagrammatic vertical section of the spermary of Nitella, showing the stalk (*stk*), four of the eight shields (*sh*), each bearing on its inner face a handle (*hn*), to which is attached a head-cell (*hd*): each head-cell bears six secondary head-cells (*hd'*), to each of which four spermatic filaments (*sp. f.*) are attached.

B, one of the proximal shields (*sh*), with handle (*hn*), head-cell (*hd*), secondary head-cells (*hd'*), and spermatic filaments (*sp. f.*).

C, a single sperm.

D^1, D^2, D^3, three stages in the development of the spermary.

(C, after Howes.)

it into eight triangular pieces. Strictly speaking, however, only the four distal shields are triangular: the four proximal ones have each its lower angle truncated by the insertion of the stalk, so that they are actually four-sided.

Each shield (Fig. 46, A and B, *sh*) is a single concavo-convex cell having on its inner surface numerous orange-coloured chromatophores: owing to the disposition of these

on the inner surface only, the spermary appears to have a colourless transparent outer layer—like an orange inclosed in a close-fitting glass case.

Attached to the middle of the inner surface of each shield is a cylindrical cell, the *handle* (*hn*), which extends towards the centre of the spermary, and, like the shield itself, contains orange chromatophores. Each of the eight handles bears a colourless *head-cell* (*hd*), to which six *secondary head cells* (*hd'*) are attached, and each of these latter bears four delicate coiled filaments (*sp. f.*) divided by septa into small cells arranged end to end, and thus not unlike the hyphæ of a fungus. There are therefore nearly two hundred of these *spermatic filaments* in each spermary, coiled up in its interior like a tangled mass of white cotton.

The cells of which the filaments are composed have at first the ordinary character, but as the spermary arrives at maturity there is produced in each a single sperm (c), having the form of a spirally-coiled thread, thicker at one end than the other, and bearing at its thin end two long flagella. In all probability the sperm proper, *i.e.*, the spirally coiled body, is formed from the nucleus of the cell, the flagella from its protoplasm. As each of the 200 spermatic filaments consists of from 100 to 200 cells, a single spermary gives rise to between 20,000 and 40,000 sperms.

When the sperms are formed the shields separate from one another and the spermatic filaments protrude between them like cotton from a pod: the sperms then escape from the containing cells and swim freely in the water.

The ovary (Fig. 44, G, *ovy*, and Fig. 47 A) is ovoidal in form, attached to the leaf by a short stalk (*stk*), and terminated distally by a little chimney-like elevation or *crown* (*cr*). It is marked externally by spiral grooves which can be

traced into the crown, and in young specimens its interior is readily seen to be occupied by a large opaque mass (*ov*). Sections show that this central body is the *ovum*, a large cell very rich in starch : it is connected with the unicellular stalk by a small cell (*nd*) from which spring five spirally-arranged cells (*sp. c*) : these coil round the ovum and their free ends —each divided by septa into two small cells—project at the distal end of the organ and form the crown, enclosing a

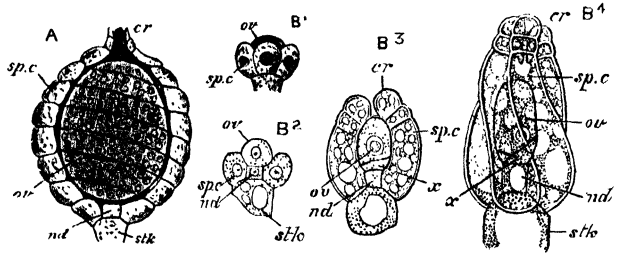

FIG. 47.—A, vertical section of the ovary of Nitella, showing the stalk (*stk*), small node (*nd*) from which spring the five spirally-twisted cells (*sp. c*), each ending in one of the two-celled sections of the crown (*cr*). The ovum contains starch grains, and is represented as transparent, the spiral cells being seen through it.

B¹, surface view, and B², section of a very young ovary : B³, later stage in vertical section : B⁴, still later stage, surface view, with the ovum seen through the transparent spiral cells. Letters as in A, except *x*, small cells formed by division from the base of the ovum. (B²–B⁴ after Sachs.)

narrow canal which places the distal end of the ovum in free communication with the surrounding water.

We saw how the various parts of the fully formed plant—nodal, and internodal cells, leaves, and rhizoids—were all formed by the modification of similar cells produced in the apical bud. It is interesting to find that the same is true of the diverse parts of the reproductive organs.

The spermary arises as a single stalked globular cell which

becomes divided into eight octants (Fig. 46, D[1]). Each of these then divides tangentially (*i.e.* parallel to the surface of the sphere) into two cells (D[2]), the inner of which divides again (D[3]), so that each octant is now composed of three cells. Of these the outermost forms the shield, the middle the handle, and the inner the head-cell: from the latter the secondary head-cells and spermatic filaments are produced by budding. The entire spermary appears to be a modified leaflet.

The ovary also arises as a single cell, but soon divides and becomes differentiated into an axial row of three cells (Fig. 47, B[2], *ov*, *nd*, *stk*) surrounded by five others (*sp. c*) which arise as buds from the middle cell of the axial row (*nd*) and are at first knob-like and upright (B[1]). The uppermost or distal cell of the axial row becomes the ovum (B[3], B[4], *ov*), the others the stalk (*stk*) and intermediate cells (*nd*, *x*): the five surrounding cells elongate, and as they do so acquire a spiral twist which becomes closer and closer as growth proceeds (compare B[1]—B[4], and Fig. 44, G, *ovy*). At the same time the distal end of each develops two septa (B[3]) and, projecting beyond the level of the ovum, forms with its fellows the chimney or crown (*cr*) of the ovary. There is every reason to believe that the entire ovary is a highly-modified shoot: the stalk representing an internode, the cell *nd* a node, the spiral cells leaves, and the ovum an apical cell.

Thus while the ciliate Infusoria and Caulerpa furnish examples of cell-differentiation without cell-multiplication, and Spirogyra of cell-multiplication without cell-differentiation, Nitella is a simple example of an organism in which complexity is obtained by the two processes going on hand in hand. It is a solid aggregate, the constituent cells of which are so arranged as to produce a well-defined external form,

while some of them undergo a more or less striking differentiation according to the position they have to occupy, and the function they have to perform.

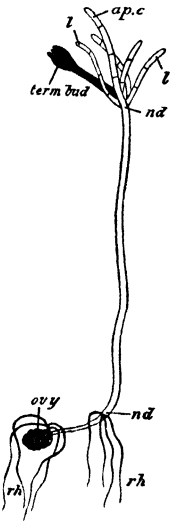

FIG. 48.—Embryo of Chara, an ally of Nitella, showing the ovary (*ovy*), from the oosperm in which the embryo has sprung: the two nodes (*nd*), apical cell (*ap. c*), rhizoids (*rh*), and leaves (*l*) of the embryo: and the rudiment of the leafy plant (shaded) ending in the characteristic terminal bud (*term. bud*). (After Howes, slightly altered.)

Impregnation takes place in the same manner as in Vaucheria (p. 173). A sperm makes its way down the canal in the chimney-like crown of cells terminating the ovary, and conjugates with the ovum converting it into an oosperm.

After impregnation the ovary, with the contained oosperm, becomes detached and falls to the bottom, where, after a

period of rest, it germinates. The process begins by the division of the oosperm into two cells, a small one nearest the crown and composed almost wholly of protoplasm, and a larger one full of starch granules. The larger cell serves simply as a store of nutriment to the growing plant which is itself developed exclusively from the small cell. The latter divides into two cells one of which grows downwards as a root-fibre, the other upwards as a shoot, consisting at first of a single row of cells (Fig. 48). Soon two nodes (*nd*) are formed on the filament, or *embryo*, from the lower of which rhizoids (*rh*) proceed, while the upper gives rise to a few leaves (*l*), and to a small process which is at first unicellular, but, behaving like an apical cell of Nitella, soon becomes a terminal bud (*term. bud*) and grows into the adult plant.

It will be seen that the development of Nitella is remarkable for the facts that the adult plant is not formed directly from the oosperm but that the latter gives rise to an embryo, quite different from the adult in structure, and that, from the embryo, the adult is finally developed as a lateral bud.

LESSON XXI

HYDRA.

We have seen that with plants, both Fungi and Algæ, the next stage of morphological differentiation after the simple unicellular or non-cellular organism is the linear aggregate. Among animals there are no forms known to exist in this stage, but coming immediately above the highest unicellular animals, such as the ciliate Infusoria, we have true solid aggregates. The characters of one of the simplest of these and the fundamental way in which it differs from the plants described in the two previous lessons will be made clear by a study of one of the little organisms known as "fresh-water polypes" and placed under the genus *Hydra*.

Although far from uncommon in pond-water, Hydra is not always easy to find, being rarely abundant and by no means conspicuous. In looking for it the best plan is to fill either a clear glass bottle or beaker or a white saucer with weeds and water from a pond and to let it remain undisturbed for a few minutes. If the gathering is successful there will be seen adhering to the sides of the glass, the bottom of the saucer, or the weeds, little white, tawny, or green bodies, about as thick as fine sewing cotton, and 2—6 mm. in length. They adhere pretty firmly by one end, and examin-

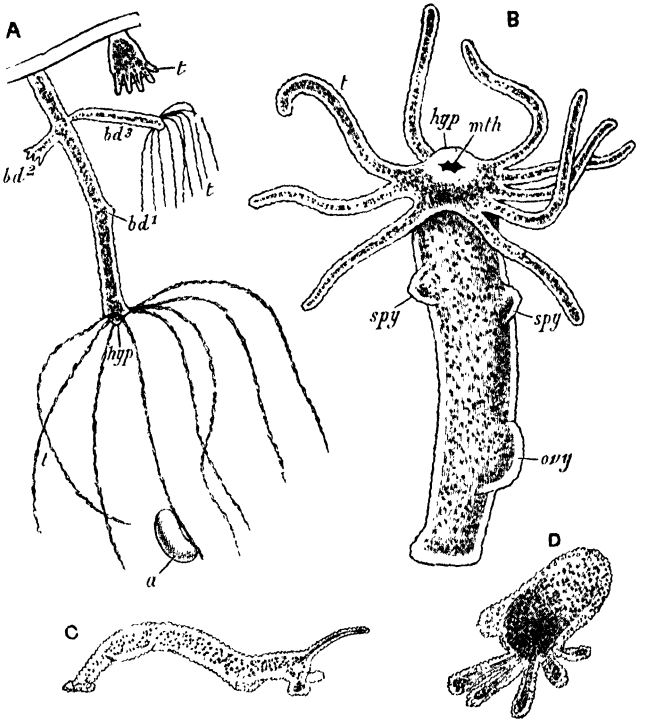

FIG. 49.—*Hydra.*

A, Two living specimens of *H. viridis* attached to a bit of weed. The larger specimen is fully expanded, and shows the elongated body ending distally in the hypostome (*hyp*), surrounded by tentacles (*t*), and three buds (bd^1, bd^2, bd^3) in different stages of development: a small water-flea (*a*) has been captured by one tentacle. The smaller specimen (to the right and above) is in a state of complete retraction, the tentacles (*t*) appearing like papillæ.

B, *H. fusca*, showing the mouth (*mth*) at the end of the hypostome (*hyp*), the circlet of tentacles (*t*), two spermaries (*spy*), and an ovary (*ovy*).

C, a Hydra creeping on a flat surface by looping movements.

D, a specimen crawling on its tentacles.

(C and D after W. Marshall.)

ation with a pocket lens shows that from the free extremity a number of very delicate filaments, barely visible to the naked eye, are given off.

Under the low power of a compound microscope a Hydra (Fig. 49, B) is seen to have a cylindrical body attached by a flattened base to a weed or other aquatic object, and bearing at its opposite or distal end a conical structure, the *hypostome* (*hyp*), at the apex of which is a circular aperture, the mouth (*mth*). At the junction of the hypostome with the body proper are given off from six to eight long delicate *tentacles* (*t*) arranged in a circlet or whorl. A longitudinal section shows that the body is hollow, containing a spacious cavity, the *enteron* (Fig. 50, A, *ent. cav*), which communicates with the surrounding water by the mouth. The tentacles are also hollow, their cavities communicating with the enteron.

There are three kinds of Hydra commonly found: one, *H. vulgaris*, is colourless or nearly so; another, *H. fusca*, is of a pinkish-yellow or brown colour; the third, *H. viridis*, is bright green. In the two latter it is quite evident, even under a low power, that the colour is in the inner parts of the body-wall, the outside of which is formed by a transparent colourless layer (Fig. 49, A, B).

It is quite easy to keep a Hydra under observation on the stage of the microscope for a considerable time by placing it in a watch-glass or shallow "cell" with weeds, &c., and in this way its habits can be very profitably studied.

It will be noticed, in the first place, that its form is continually changing. At one time (Fig. 49, A, left-hand figure) it extends itself until its length is fully fifteen times its diameter and the tentacles appear like long delicate filaments: at another time (right-hand figure) it contracts itself into an almost globular mass, the tentacles then appearing like little blunt knobs.

Besides these movements of contraction and expansion, Hydra is able to move slowly from place to place. This it usually does after the manner of a looping caterpillar (Fig. 49, C): the body is bent round until the distal end touches the surface: then the base is detached and moved nearer the distal end, which is again moved forward, and so on. It has also been observed to crawl like a cuttle fish (D) by means of its tentacles, the body being kept nearly vertical.

It is also possible to watch a Hydra feed. It is a very voracious creature, and to see it catch and devour its prey is a curious and interesting sight. In the water in which it lives are always to be found numbers of "water-fleas," minute animals .from about a millimetre downwards in length, belonging to the class *Crustacea*, a group which includes lobsters, crabs, shrimps, &c.

Water-fleas swim very rapidly, and occasionally one may be seen to come in contact with a Hydra's tentacle. Instantly its hitherto active movements stop dead, and it remains adhering in an apparently mysterious manner to the tentacle. If the Hydra is not hungry it usually liberates its prey after a time, and the water-flea may then be seen to drop through the water like a stone for a short distance, but finally to expand its limbs and swim off. If however the Hydra has not eaten recently it gradually contracts the tentacle until the prey is brought near the mouth, the other tentacles being also used to aid in the process. The water-flea is thus forced against the apex of the hypostome, the mouth expands widely and seizes it, and it is finally passed down into the digestive cavity. Hydræ can often be seen with their bodies bulged out in one or more places by recently swallowed water-fleas.

The precise structure of Hydra is best made out by cutting

it into a series of extremely thin sections and examining them under a high power. The appearance presented by a vertical section through the long axis of the body is shown in Fig. 50.

The whole animal is seen to be built up of cells, each consisting of protoplasm with a large nucleus (B, C, *nu*), and with or without vacuoles. As in the case of most animal cells, there is no cell-wall. Hydra is therefore a solid aggregate: but the way in which its constituent cells are arranged is highly characteristic and distinguishes it at once from a plant.

The essential feature in the arrangement of the cells is that they are disposed in two layers round the central digestive cavity or enteron (A, *ent. cav*) and the cavities of tentacles (*ent. cav'*). So that the wall of the body is formed throughout of an outer layer of cells, the *ectoderm* (*ect*), and of an inner layer, the *endoderm* (*end*), which bounds the enteric cavity. Between the two layers is a delicate transparent membrane, the *mesoglœa*, or *supporting lamella* (*msgl*). A transverse section shows that the cells in both layers are arranged radially (B).

Thus Hydra is a two-layered or *diploblastic* animal, and may be compared to a chimney built of two layers of radially arranged bricks with a space between the layers filled with mortar or concrete.

Accurate examination of thin sections, and of specimens teased out or torn into minute fragments with needles, shows that the structure is really much more complicated than the foregoing brief description would indicate.

The ectoderm cells are of two kinds. The first and most obvious (B, *ect* and C), are large cells of a conical form, the bases of the cones being external, their apices internal. Spaces

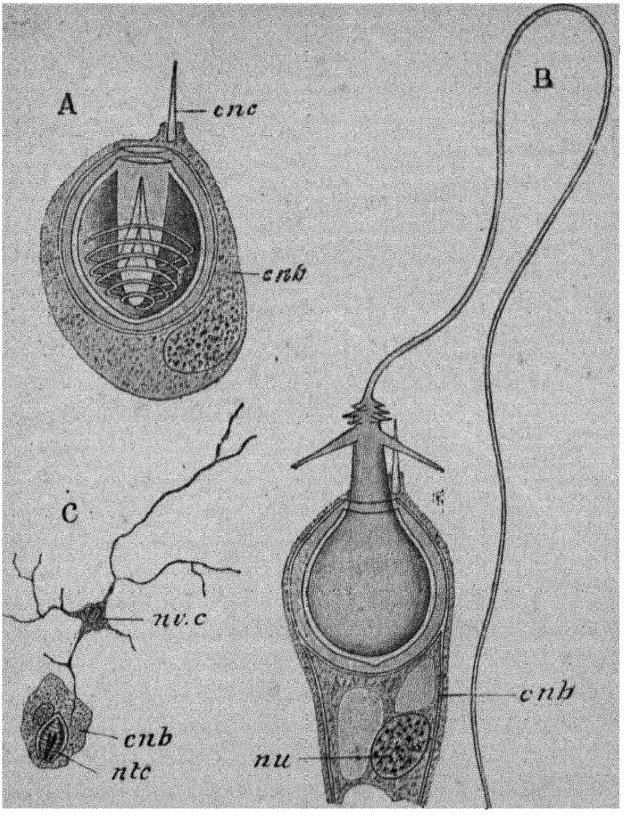

FIG. 51. — *Hydra.*

A, A nematocyst contained in its cnidoblast (*cnb*), showing the coiled filament and the cnidocil (*cnc*).

B, The same after extrusion of the thread, showing the larger and smaller barbs at the base of the thread. *nu*, the nucleus of the cnidoblast.

C, A cnidoblast, with its contained nematocyst, connected with one of the processes of a nerve-cell (*nv. c*).

(After Schneider.)

degree of contractility is assigned to the muscle-processes while the cells themselves are eminently irritable, the slightest stimulus applied to them being followed by an immediate contraction of the whole body.

Imbedded in some of the large ectoderm cells are found clear, oval sacs (A and B, *ntc*), with very well-defined walls and called *nematocysts*. Both in the living specimen and in sections they ordinarily present the appearance shown in Fig. 50, B. *ntc*, and Fig. 51 A, but are frequently met with in the condition shown in Fig. 50 E, and Fig. 51 B: that is, with a short conical tube protruding from the mouth of the sac, armed near its distal end with three recurved barbs besides several similar processes of smaller size, and giving rise distally to a long, delicate, flexible filament.

Accurate examination of the nematocysts shows that the structure of these curious bodies is as follows. Each consists of a tough sac (Fig. 51, A), one end of which is turned in as a hollow pouch : the free end of the latter is continued into a hollow coiled filament, and from its inner surface project the barbs. The whole space between the wall of the sac and the contained pouch and thread is tensely filled with fluid. When pressure is brought to bear on the outside of the sac the whole apparatus goes off like a harpoon-gun (B), the compression of the fluid forcing out first the barbed pouch and then the filament, until finally both are turned inside out.

It is by means of the nematocysts—the resemblance of which to the trichocysts of Paramœcium (p. 113) should be noted—that the Hydra is enabled to paralyze its prey. Probably some specific poison is formed and ejected into the wound with the thread : in the larger members of the group to which Hydra belongs, such as jelly-fishes, the nematocysts

produce an effect on the human skin quite like the sting of a nettle.

The nematocysts are formed in special interstitial cells called *cnidoblasts* (Fig. 50, B, *cnbl* and Fig. 51), and are thus in the first instance at a distance from the surface. But the cnidoblasts migrate outwards, and so come to lie quite superficially either in or between the large ectoderm cells. On its free surface the cnidoblast is produced into a delicate pointed process, the *cnidocil* or "trigger-hair" (*cnc*). In all probability the slightest touch of the cnidocil causes contraction of the cnidoblast, and the nematocyst, thus compressed, instantly explodes.

Nematocysts are found in the distal part of the body, but are absent from the foot or proximal end, where also there are no interstitial cells. They are especially abundant in the tentacles, on the knob-like elevations of which—due to little heaps of interstitial cells—they are found in great numbers. Amongst these occur small nematocysts with short threads and devoid of barbs (Fig. 50, A, *ntc'* and F).

There are sometimes found in connection with the cnidoblasts small irregular cells with large nuclei: they are called *nerve-cells* (Fig. 51, C, *nv. c*), and constitute a rudimentary *nervous system*, the nature of which will be more conveniently discussed in the next lesson (p. 242).

The ectoderm cells of the foot differ from those of the rest of the body in being very granular (Fig. 50 A). The granules are probably the material of the adhesive substance by which the Hydra fixes itself, and are to be looked upon as products of destructive metabolism: *i.e.* as being formed by conversion of the protoplasm in something the same way as starch granules (p. 33). This process of formation in a cell of a definite product which accumulates and is finally discharged at the free surface of the cell is called *secretion*,

and the cell performing the function is known as a *gland-cell.*

The endoderm consists for the most part of large cells which exceed in size those of the ectoderm, and are remarkable for containing one or more vacuoles, sometimes so large as to reduce the protoplasm to a thin superficial layer containing the nucleus (Fig. 50, A and B, *end*). Then again, their form is extremely variable, their free or inner ends undergoing continual changes of form. This can be easily made out by cutting transverse sections of a living Hydra, when the endoderm cells are seen to send out long blunt pseudopods (*psd*) into the digestive cavity, and now and then to withdraw the pseudopods and send out from one to three long delicate flagella (*fl*). Thus the endoderm cells of Hydra illustrate in a very instructive manner the essential similarity of flagella and pseudopods already referred to (p. 52). In the hypostome the endoderm is thrown into longitudinal folds, so as to allow of the dilatation of the mouth in swallowing.

Amongst the ordinary endoderm-cells are found long narrow cells of an extremely granular character. They are specially abundant in the distal part of the body, beneath the origins of the tentacles, and in the hypostome, but are absent in the tentacles and in the foot. There is no doubt that they are gland-cells, their secretion being a fluid used to aid in the digestion of the food.

In Hydra viridis the endoderm-cells (D) contain chromatophores (*chr*) coloured green by chlorophyll, which performs the same function as in plants, so that in this species holozoic is supplemented by holophytic nutrition. There is reason for believing that the chromatophores are to be regarded as symbiotic algæ, like those found in connection with Radio-

laria (p. 154). In H. fusca bodies resembling these chromatophores are present, but are of an orange or brown colour, and devoid of chlorophyll. Brown and black granules occurring in the cells (B) seem to be due in part to the degeneration of the chromatophores, and in part to be products of excretion.

Muscle-processes exist in connection with the endoderm cells, and they are said to take a transverse or circular direction, *i.e.*, at right angles to the similar processes of the ectoderm cells.

When a water-flea or other minute organism is swallowed by a Hydra, it undergoes a gradual process of disintegration. The process is begun by a solution of the soft parts due to the action of a digestive fluid secreted by the gland-cells of the endoderm; it is apparently completed by the endoderm cells seizing minute particles with their pseudopods and engulfing them quite after the manner of Amœbæ. It is often found that the protrusion of pseudopods during digestion results in the almost complete obliteration of the enteric cavity.

It would seem therefore that in Hydra the process of digestion or solution of the food is to some extent at least *intra-cellular*, *i.e.*, takes place in the interior of the cells themselves, as in Amœba or Paramœcium: it is however mainly *extra-cellular* or *enteric i.e.*, is performed in a special digestive cavity lined by cells.

The ectoderm cells do not take in food directly, but are nourished entirely by diffusion from the endoderm. Thus the two layers have different functions: the ectoderm is protective and sensory; it forms the external covering of the animal, and receives impressions from without; the endoderm, removed from direct communication with the outer world, performs a nutrient function, its cells alone having the power of digesting food.

The essential difference between digestion and assimilation is here plainly seen: all the cells of Hydra assimilate, all are constantly undergoing waste, and all must therefore form new protoplasm to make good the loss. But it is the endoderm cells alone which can make use of raw or undigested food: the ectoderm has to depend upon various products of digestion received by osmosis from the endoderm.

It will be evident from the preceding description that Hydra is comparable to a colony of Amœbæ in which particular functions are made over to particular individuals—just as in a civilized community the functions of baking and butchering are assigned to certain members of the community, and not performed by all. Hydra is therefore an example of *individuation:* morphologically it is equivalent to an indefinite number of unicellular organisms: but, these acting in concert, some taking one duty and some another, form, physiologically speaking, not a colony of largely independent units, but a single multicellular individual.

Like many of the organisms which have come under our notice, Hydra has two distinct methods of reproduction, asexual and sexual.

Asexual multiplication takes place by a process of budding. A little knob appears on the body (Fig. 49, A, bd^1), and is found by sections to arise from a group of ectoderm cells; soon however it takes on the character of a hollow outpushing of the wall containing a prolongation of the enteron, and made up of ectoderm, mesogloea, and endoderm. (Fig. 50, A, bd^1). In the course of a few hours this prominence enlarges greatly, and near its distal end six or eight hollow buds appear arranged in a whorl (Fig. 49, A, bd^2; Fig. 50,

A, *bd*^{2}). These enlarge and take on the characters of tentacles: a mouth is formed at the distal end of the bud, which thus acquires the character of a small Hydra (Fig. 49, A, *bd*^{3}). Finally the bud becomes constricted at its base, separates from the parent, and begins an independent existence. Sometimes, however, several buds are produced at one time, and each of these buds again before becoming detached: in this way temporary colonies are formed. But the buds always separate sooner or later, although they frequently begin to feed while still attached.

It is a curious circumstance that Hydra can also be multiplied by artificial division: the experiment has been tried of cutting the living animal into pieces, each of which was found to grow into a perfect individual.

As in Vaucheria and Nitella, the sexual organs or gonads are of two kinds, spermaries and ovaries. Both are found in the same individual, Hydra being, like the plants just mentioned, *hermaphrodite* or *monœcious*.

The spermaries (Fig. 49, B, and Fig. 50, A, *spy*) are white conical elevations situated near the distal end of the body: as a rule not more than one or two are present at the same time, but there may be as many as twenty. They are perfectly colourless, even in the green and brown species, being obviously formed of ectoderm alone.

In the immature condition the spermary consists of a little heap of interstitial cells covered by an investment of somewhat flattened cells formed by a modification of the ordinary large cells of the ectoderm. When mature each of the small internal cells becomes converted into a sperm (Fig. 50, G), consisting of a small ovoid head formed from the nucleus of the cell, and of a long vibratile tail formed from its protoplasm. By the rupture of the investing cells or wall of the

spermary the sperms are liberated and swim freely in the water.

The ovaries (Fig. 49, B, and Fig. 50, A, *ovy*) are found near the proximal end of the body, and vary in number from one to eight. When ripe an ovary is larger than a spermary, and of a hemispherical form. It begins, like the spermary, as an aggregation of interstitial cells, so that in their earlier stages the sex of the gonads is indeterminate. But while

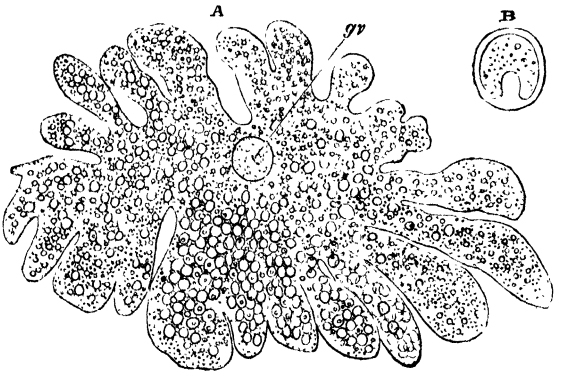

FIG. 52.—A, Ovum of *Hydra viridis*, showing pseudopods, nucleus (*gv*), and numerous chromatophores and yolk spheres.
B, a single yolk sphere. (From Balfour after Kleinenberg.)

in the spermary each cell is converted into a sperm, in the ovary one cell soon begins to grow faster than the rest becomes amœboid in form (Fig. 50, A, *ov*, and Fig. 52, A), sending out pseudopods amongst its companions and ingesting the fragments into which they become broken up, thus continually increasing in size at their expense. Ultimately the ovary comes to consist of this single amœboid *ovum*, and of a layer of superficial cells forming a capsule for it.

As the ovum grows *yolk-spheres* (Fig. 52), small rounded masses of proteid material, are formed in it, and in Hydra viridis it also acquires green chromatophores.

When the ovary is ripe the ovum draws in its pseudopods and takes on a spherical form: the investing layer then bursts so as to lay bare the ovum and allow of the free access to it of the sperms. One of the latter conjugates with the ovum, producing an *oosperm* or unicellular embryo.

The oosperm divides into a number of cells, the outermost of which becomes changed into a hard shell or capsule. The embryo, thus protected, falls to the bottom of the water, and after a period of rest develops into a Hydra. As, however, there are certain abnormal features about the development of this genus which cannot well be understood by the beginner, it will not be described in detail, but the very important series of changes by which the oosperm of a multicellular animal becomes converted into the adult will be considered in the next lesson.

LESSON XXII.

HYDROID POLYPES :—BOUGAINVILLEA, DIPHYES, AND PORPITA.

It was stated in the previous lesson (p. 231) that in a budding Hydra the buds do not always become detached at once, but may themselves bud while still in connection with the parent, temporary colonies being thus produced.

Suppose this state of things to continue indefinitely: the result would be a tree-like colony or compound organism consisting of a stem with numerous branchlets each ending in a Hydra-like zooid. Such a colony would bear much the same relation to Hydra as Zoothamnium bears to Vorticella (see p. 134).

As a matter of fact this is precisely what happens in a great number of animals allied to Hydra and known by the name of *Zoophytes* or *Hydroid polypes*.

Every one is familiar with the common Sertularians of the sea-coast, often mistaken for sea-weeds: they are delicate, much-branched, semi-transparent structures of a horny consistency, the branches beset with little cups, from each of which, during life, a Hydra-like body is protruded.

A very convenient genus of hydroid polypes for our purpose is *Bougainvillea*, found in the form of little tufts a few centimetres long attached to rocks and other submarine

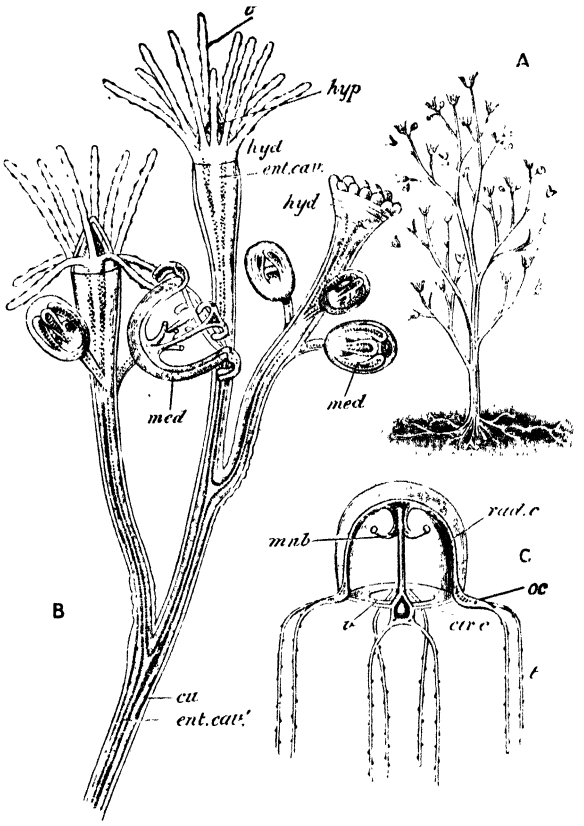

FIG. 53.—*Bougainvillea ramosa.*

A, a complete living colony of the natural size, showing the branched stem and root-like organ of attachment.

B, a portion of the same magnified, showing the branched stem bearing hydranths (*hyd*) and medusæ (*med*), one of the latter nearly mature, the others undeveloped : each hydranth has a circlet of tentacles (*t*) surrounding a hypostome (*hyp*), and contains an enteric cavity (*ent. cav*) continuous with a narrow canal (*ent. cav'*) in the stem. The stem is covered by a cuticle (*cu*).

C, a medusa after liberation from the colony, showing the bell with tentacles (*t*), velum (*v*), manubrium (*mnb*), radial (*rad. c*) and circular (*cir. c*) canals, and eye-spots (*oc*). (After Allman.)

objects. Fig. 53, A, shows a colony of the natural size, B a part of it magnified: it consists of a much-branched stem of a yellowish colour attached by root-like fibres to the support. The branches terminate in little Hydra-like bodies called *hydranths* (B, *hyd*), each with a hypostome (*hyp*) and circlet of tentacles (*t*). Lateral branchlets bear bell-shaped structures or *medusæ* (*med*): these will be considered presently.

Sections show that the hydranths have essentially the structure of a Hydra, consisting of a double layer of cells —ectoderm and endoderm - separated by a supporting lamella or mesogloea, and enclosing a digestive cavity (*ent. cav*) which opens externally by a mouth placed at the summit of the hypostome.

The tentacles, however, differ from those of Hydra in two important respects. In the first place they are solid: the endoderm instead of forming a lining to a prolongation of the enteron, consists (Fig. 55, *end.*) of a single axial row of large cells with thick cell-walls and vacuolated protoplasm. Then in the position of the muscle-processes of Hydra there is a layer of spindle-shaped fibres (*m.f.*), many times longer than broad, and provided each with a nucleus. Such *muscle-fibres* are obviously cells greatly extended in length, so that the ectoderm cell of Hydra with its continuous muscle-*process* is here represented by an ectoderm cell with an adjacent muscle-*cell*. We thus get a partial intermediate layer of cells between the ectoderm and endoderm in addition to the gelatinous mesogloea, and so, while a hydroid polyp is, like Hydra, *diploblastic* (p. 222), it shows a tendency towards the assumption of a three-layered or *triploblastic* condition.

The stem is formed of the same layers and contains a cavity (*ent. cav'*) continuous with those of the hydranths, and thus the structure of a hydroid polype is, so far, simply

that of a Hydra in which the process of budding has gone on to an indefinite extent and without separation of the buds.

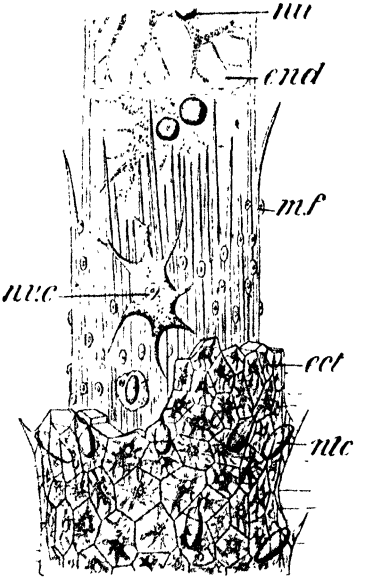

FIG. 54.—Portion of the tentacle of a Zoophyte (*Eucopella*).
In the lower part of the figure are seen the ectoderm cells (*ect*) with the nematocysts (*ntc*). In the middle part the ectoderm is removed, and the muscle-fibres (*m. f*) and nerve-cells (*nv. c*) are exposed. In the upper part the muscular and nervous layer is removed, and parts of two endoderm cells (*end*) are shown ; *mt*, nucleus.
(From Parker and Haswell, after von Lendenfeld.)

There is however an additional layer added in the stem for protective and strengthening purposes. It is evident that a colony of the size shown in Fig. 53, A, would, if formed

only of soft ectodermal and endodermal cells, be so weak as to be hardly able to bear its own weight even in water. To remedy this a layer of transparent, yellowish substance of horny consistency, called the *cuticle*, is developed outside the ectoderm of the stem, extending on to the branches and only stopping at the bases of the hydranths and medusæ. It is this layer which, when the organism dies and decays, is left as a semi-transparent branched structure resembling the living colony in all but the absence of hydranths and medusæ. The cuticle is therefore a supporting organ or skeleton, not, like our own bones, formed in the interior of the body (*endoskeleton*), but like the shell of a crab or lobster lying altogether outside the soft parts (*exoskeleton*).

As to the mode of formation of the cuticle:—we saw that many organisms, such as Amœba and Hæmatococcus, form, on entering into the resting condition, a cyst or cell-wall, by secreting or separating from the surface of their protoplasm a succession of layers either of cellulose or of a transparent horn-like substance. But Amœba and Hæmatococcus are unicellular, and are therefore free to form this protective layer at all parts of their surface. The ectoderm cells of Bougainvillea on the other hand are in close contact with their neighbours on all sides and with the mesoglœa at their inner ends, so that it is not surprising to find the secretion of skeletal substance taking place only at their outer ends. As the process takes place simultaneously in adjacent cells, the result is a continuous layer common to the whole ectoderm instead of a capsule to each individual cell. It is to an exoskeletal structure formed in this way, *i.e.* by the secretion of successive layers from the free faces of adjacent cells, that the name cuticle is in strictness applied in multicellular organisms.

The medusæ (B, *med,* and C), mentioned above as occurring on lateral branches of the colony, are found in various stages of development, the younger ones having a nearly globular shape, while when fully formed each resembles a bell attached by its handle to one of the branches of the colony and having a clapper in its interior. When quite mature the medusæ become detached and swim off as little jelly-fishes (C).

The structure of a medusa must now be described in some detail. The bell or *umbrella* (C) is formed of a gelatinous substance (Fig. 55, D, *msgl*) covered on both its inner surface or *sub-umbrella* and on its outer surface or *ex-umbrella* by a thin layer of delicate cells (*ect*). The clapper-like organ or *manubrium* (Fig. 53, C and Fig. 55 D and D', *mnb*) is formed of two layers of cells, precisely resembling the ectoderm and endoderm of Hydra, and separated by a thin mesogloea; it is hollow, its cavity (Fig. 55, D, *ent. cav*) opening below, *i.e.* at its distal or free end, by a rounded aperture, the *mouth* (*mth*), used by the medusa for the ingestion of food. At its upper (attached or proximal) end the cavity of the manubrium is continued into four narrow, *radial canals* (Fig. 53, C, *rad. c*, and Fig. 54, D and D' *rad*) which extend through the gelatinous substance of the umbrella at equal distances from one another, like four meridians, and finally open into a *circular canal* (*cir. c*) which runs round the edge of the umbrella. The whole system of canals is lined by a layer of cells (Fig. 55, D and D', *end*) continuous with the inner layer or endoderm of the manubrium; and extending from one canal to another in the gelatinous substance of the umbrella is a delicate sheet of cells, the *endoderm-lamella* (D', *end. la*).

From the edge of the umbrella four pairs of tentacles (Fig. 53, C and Fig. 55, D, *t*) are given off, one pair corres-

ponding to each radial canal, and close to the base of each tentacle is a little speck of pigment (Fig. 53, *oc*), the *ocellus* or eye-spot. Lastly, the margin of the umbrella is continued inwards into a narrow circular shelf, the *velum* (*v*).

At first sight there appears to be very little resemblance between a medusa and a hydranth, but it is really quite easy to derive the one form from the other.

Suppose a simple polype or Hydra-like body with four tentacles (Fig. 55, A, A′) to have the region from which the tentacles spring pulled out so as to form a hollow, transversely extended disc (B). Next, suppose this disc to become bent into the form of a cup with its concavity towards the hypostome, and to undergo a great thickening of its mesogloea. A form would be produced like C, *i.e.* a medusa-like body with umbrella and manubrium, but with a continuous cavity (c′, *ent. cav*′) in the thickness of the umbrella instead of four radial canals. Finally, suppose the inner and outer walls of this cavity to grow towards one another and meet, thus obliterating the cavity, except along four narrow radial areas (D, *rad*) and a circular area near the edge of the umbrella (D, *cir. c*). This would result in the substitution for the continuous cavity of four radial canals opening on the one hand into a circular canal and on the other into the cavity of the manubrium (*ent. cav*), and connected with one another by a membrane—the endoderm-lamella (*end. la*)—indicating the former extension of the cavity.

It follows from this that the inner and outer layers of the manubrium are respectively endoderm and ectoderm: that the gelatinous tissue of the umbrella is an immensely thickened mesogloea: that the layer of cells covering both inner and outer surfaces of the umbrella is ectodermal: and that the layer of cells lining the system of canals, together with the endoderm-lamella, is endodermal.

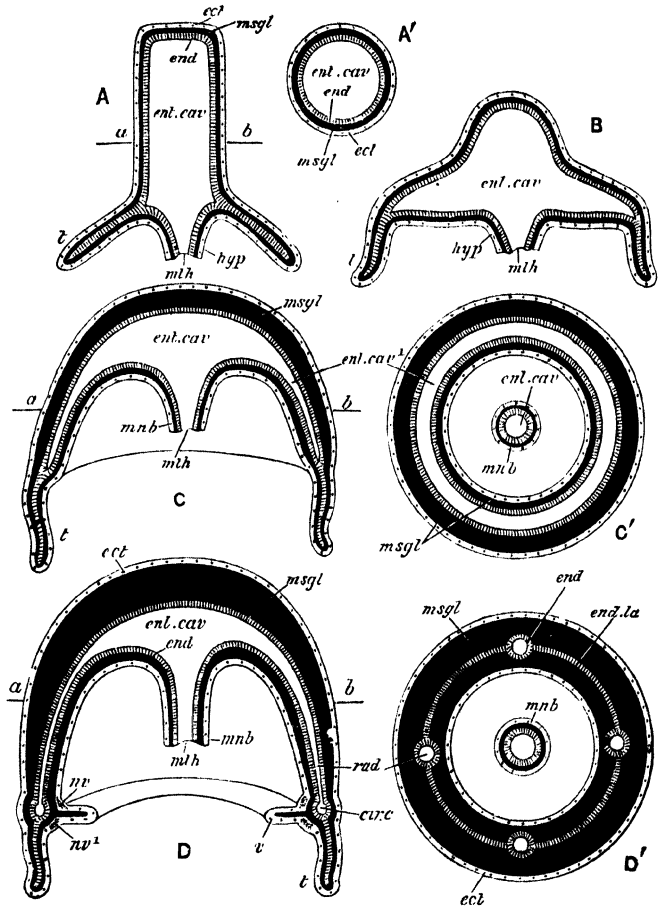

FIG. 55.—Diagrams illustrating the derivation of the medusa from the hydranth. In the whole series of figures the ectoderm (*ect*) is dotted, the endoderm (*end*) striated, and the mesogloea (*msgl*) black.

A, longitudinal section of a simple polype, showing the tubular body with enteric cavity (*ent. cav*), hypostome (*hyp*), mouth (*mth*), and tentacles (*t*).

A', transverse section of the same through the plane *a b*.

B, the tentacular region is extended into a hollow disc.

C, the tentacular region has been further extended and bent into a bell-like form, the enteric cavity being continued into the umbrella (*ent. cav'*) : the hypostome now forms a manubrium (*mnb*).

C', transverse section of the same through the plane *a b*, showing the continuous cavity (*ent. cav'*) in the umbrella.

D, fully formed medusa : the cavity in the umbrella is reduced to the radiating (*rad*) and circular (*cir. c*) canals, the velum (*v*) is formed, and a double nerve-ring (*nv, nv'*) is produced from the ectoderm.

D', transverse section of the same through the plane *a b*, showing the four radiating canals (*rad*) united by the endoderm-lamella (*end. la*), produced by partial obliteration of the continuous cavity *ent. cav'* in C'.

Thus the medusa and the hydranth are similarly constructed or *homologous* structures, and the hydroid colony, like Zoothamnium (p. 136), is dimorphic, bearing zooids of two kinds.

Sooner or later the medusæ separate from the hydroid colony and begin a free existence. Under these circumstances the rhythmical contraction—*i.e.* contraction taking place at regular intervals—of the muscles of the umbrella causes an alternate contraction and expansion of the whole organ, so that water is alternately pumped out of and drawn into it. The obvious result of this is that the medusa is propelled through the water by a series of jerks. The movement is performed by means of the muscle-processes and muscle-fibres of the sub-umbrella and velum, both of which differ from the similar structures in the hydranth in exhibiting a delicate transverse striation (Fig. 57).

There is still another important matter in the structure of the medusa which has not been referred to. At the junction of the velum with the edge of the bell there lies, immediately beneath the ectoderm, a layer of peculiar branched cells (Fig. 56, B, *n. c*), containing large nuclei and produced into long fibre-like processes. These *nerve-cells* (see p. 227)

are so disposed as to form a double ring round the margin of the bell, one ring (Fig. 55, D, *nv*) being immediately above, the other (*nv'*) immediately below the insertion of the velum. An irregular network of similar cells and fibres occurs on the inner or concave face of the umbrella, between the ectoderm and the layer of muscle-fibres. The whole consti-

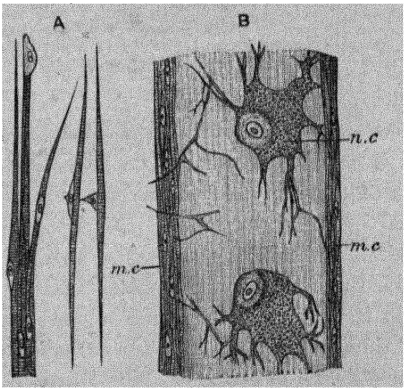

FIG. 56.—A, Muscle fibres from the inner face of the bell of the medusa of a hydroid polype (*Eucopella campanularia*), showing nucleus and transverse striation.

B, portion of the nerve-ring of the same, showing two large nerve-cells (*n. c*) and muscle-fibres (*m. c*) on either side. (After von Lendenfeld.)

tutes the *nervous system* of the medusa; the double nerve-ring is the *central*, the network the *peripheral* nervous system.

Some of the processes of the nerve-cells are connected with ordinary ectoderm-cells, which thus as it were connect the nervous system with the external world: others, in some instances at least, are probably directly connected with muscle-fibres.

We thus see that while the manubrium of a medusa has the same simple structure as a hydranth, or what comes to

the same thing, as a Hydra, the umbrella has undergone a very remarkable differentiation of its tissues. Its ordinary ectoderm cells, instead of being large and eminently contractile, form little more than a thin cellular skin or *epithelium* over the gelatinous mesogloea: they have largely given up the function of contractility to the muscle processes or fibres, and have taken on the functions of a protective and sensitive layer.

Similarly the function of automatism, possessed by the whole body of Hydra, is made over to the group of specially modified ectodermal cells which constitute the central nervous system. If a Hydra is cut into any number of pieces, each of them is able to perform the ordinary movements of expansion and contraction, but if the nerve-ring of a medusa is removed by cutting away the edge of the umbrella, the rhythmical swimming movements stop dead: the bell is in fact permanently paralysed.

It is not, however, rendered incapable of movement, for a sharp pinch, *i.e.* an external stimulus, causes a single contraction, showing that the muscles still retain their irritability. But no movement takes place without such external stimulus, each stimulus giving rise infallibly to one single contraction: the power possessed by the entire animal of independently originating movement, *i.e.* of supplying its own stimuli, is lost with the central nervous system.

Another instance of morphological and physiological differentiation is furnished by the pigment spots or ocelli (Fig. 53, C, *oc*) situated at the bases of the tentacles. They consist of groups of ectoderm cells in which are deposited granules of deep red pigment. Their function is proved by the following experiment.

If a number of medusæ are placed in a glass vessel of water in a dark room, and a beam of light from a lantern is

allowed to pass through the water, the animals are all found to crowd into the beam, thus being obviously sensitive to and attracted by light. If however the ocelli are removed this is no longer the case: the medusæ do not make for the beam of light, and are incapable of distinguishing light from darkness. The ocelli are therefore organs of sight.

In Zoothamnium we saw that the two forms of zooid were respectively nutritive and reproductive in function, the reproductive zooids becoming dêtached and swimming off to found a new colony elsewhere (p. 136).

This is also the case with Bougainvillea: the hydranths are purely nutritive zooids, the medusæ, although capable of feeding, are specially distinguished as reproductive zooids. The gonads are found in the walls of the manubrium, between the ectoderm and endoderm, some medusæ producing ovaries, others spermaries only. Thus while Hydra is *monœcious*, both male and female gonads occurring in the same individual, Bougainvillea is *diœcious*, certain individuals producing only male, others only female products.

In some Hydroids it has been found that the sexual cells from which the ova and sperms are developed do not originate in the manubrium of a medusa, but arise in the first instance from the ectoderm of the stem ơ the hydroid colony, afterwards migrating, while still small and immature, to their permanent situation where they undergo their final development. In Bougainvillea, however, the reproductive products are said to originate in the manubrium.

The medusæ, when mature, become detached and swim away from the hydroid colony. The sperms of the males are shed into the water and carried to the ovaries of the females, where they fertilize the ova, converting them, as usual, into oosperms.

The changes by which the oosperm or unicellular embryo of a hydroid polype is converted into the adult are very remarkable.

The process is begun by the oosperm, still enclosed within the body of the parent (Fig. 57, A), undergoing binary fission, so that a two-celled embryo is formed (B). Each of the two cells again divides (C), and the process is repeated, the embryo consisting successively of 2, 4, 8, 16, 32, &c., cells, until a solid globular mass of small cells is produced (D, E) by the repeated division of the one large cell which forms the starting-point of the series. The embryo in this stage has been compared to a mulberry, and is called the *morula* or *polyplast*.

So far all the cells of the polyplast are alike—globular nucleated masses of protoplasm squeezed into a polyhedral form by mutual pressure. But before long the cells lying next the surface alter their form, becoming cylindrical, with their long axes disposed radially (F). In this way a superficial layer of cells, or *ectoderm*, is differentiated from an internal mass, or *endoderm*.

The embryo now assumes an elongated form (G) and begins to exhibit slow, worm-like movements, finally escaping from the parent and beginning a free existence (H). The ectoderm cells are now found to be ciliated, and before long a cavity appears in the previously solid mass of endoderm cells: this is the first appearance of the enteron or digestive cavity. In this stage the embryo is called a *planula*: it swims slowly through the water by means of its cilia, the broader end being directed forwards in progression. It then loses its cilia and settles down on a rock, shell, sea-weed, or other submarine object, assuming a vertical position with its broader end fixed to the support (I).

The attached or proximal end widens into a disc of attach-

ment, a dilatation is formed a short distance from the free or

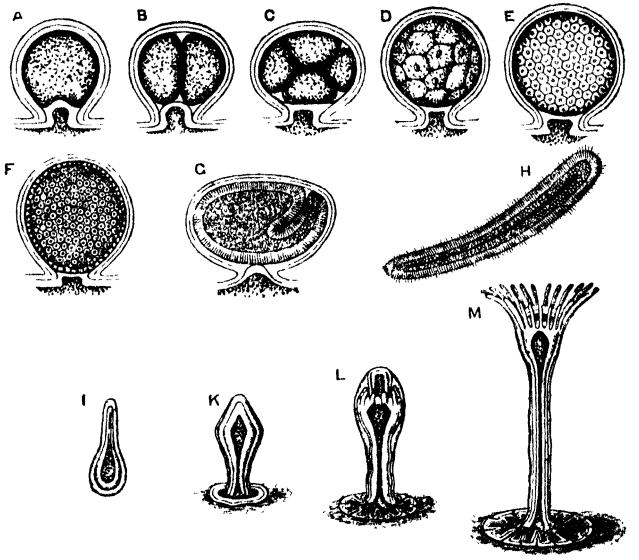

FIG. 57.—Stages in the development of two hydroid polypes, *Laomedea flexuosa* (A–H) and *Eudendrium ramosum* (I–M).

A, oosperm.

B, two-celled, and C, four-celled stage.

D, E, polyplast.

F, G, formation of planula by differentiation of ectoderm and endoderm.

In A–G the embryo is embedded in the maternal tissues.

H, free swimming planula, showing ciliated ectoderm, and endoderm enclosing a narrow enteric cavity.

I, planula, after loss of its cilia, about to affix itself.

K, the same after fixation.

L, Hydra-like stage, still enclosed in cuticle.

M, the same after rupture of the cuticle and liberation of the tentacles. (After Allman.)

distal end, and a thin cuticle is secreted from the whole surface of the ectoderm (K). From the dilated portion

short buds arise in a circle: these are the rudiments of the tentacles: the narrow portion beyond their origin becomes the hypostome (L). Soon the cuticle covering the distal end is ruptured so as to set free the growing tentacles (M): an aperture, the mouth, is formed at the end of the hypostome, and the young hydroid has very much the appearance of a Hydra with a broad disc of attachment, and with a cuticle covering the greater part of the body.

Extensive budding next takes place, the result being the formation of the ordinary hydroid colony.

Thus from the oosperm or impregnated egg-cell of the medusa the hydroid colony arises, while the medusa is produced by budding from the hydroid colony. We have what is called an *alternation of generations*, the *asexual generation* or *agamobium* (hydroid colony) giving rise by budding to the *sexual generation* or *gamobium* (medusa), which in its turn produces the agamobium by a sexual process, *i.e.* by the conjugation of ovum and sperm.

Two other Hydroids must be briefly referred to in concluding the present lesson.

Floating on the surface of the ocean in many parts of the world is found a beautiful transparent organism called *Diphyes*. It consists of a long, slender stem (Fig. 58, A, *a*), at one end of which are attached two structures called *swimming-bells* (*m*, *m*) in form something like the bowl of a German pipe, while all along the stem spring at intervals groups of structures (*e*), one of which is shown on an enlarged scale at B.

Each group contains, first, a tubular structure (B, *n*) with an expanded, trumpet-like mouth, through which food is taken: this is clearly a hydranth. From the base of the hydranth proceeds a single, long, branched tentacle or

"grappling-line" (*t*), abundantly provided with nematocysts. Springing from the stem near the base of the hydranth is a body called a medusoid (*g*), very like a sort of imperfect medusa, and like it, containing gonads. Lastly, enclosing all these structures, much as the white petaloid bract of the common Arum-lily encloses the flower-stalk, is a delicate folded membranous plate (*t*), to which the name *bract*, borrowed from botany, is applied. The whole organism is propelled through the water by the rhythmical contraction of the swimming-bells.

Microscopic examination shows that the stem consists, like that of Bougainvillea, of ectoderm, mesoglœa, and endoderm, but without a cuticle. The hydranth has a similar structure to that of Bougainvillea, only differing in shape and in the absence of tentacles round the mouth: the grappling lines are formed on the polype-type: the medusoids are merely simplified medusæ: the swimming-bells are practically medusæ in which the manubrium is absent: and the bracts are shown by comparison with allied forms to be greatly modified medusa-like structures.

Diphyes is in fact a free-swimming hydroid colony which, instead of being dimorphic like Bougainvillea, is *polymorphic*. In addition to nutritive zooids or hydranths, it possesses locomotive zooids or swimming-bells, protective zooids or bracts, and tentacular zooids or grappling-lines. Morphological and physiological differentiation are thus carried much further than in such a form as Bougainvillea.

Porpita is another free-swimming Hydroid, presenting at first sight no resemblance whatever to Diphyes. It has much the appearance of a flattened medusa (Fig. 59), consisting of a circular disc, slightly convex above and concave below, bearing round its edge a number of close-set tentacles, and on its under side a central tubular organ (*hy*) with a ter-

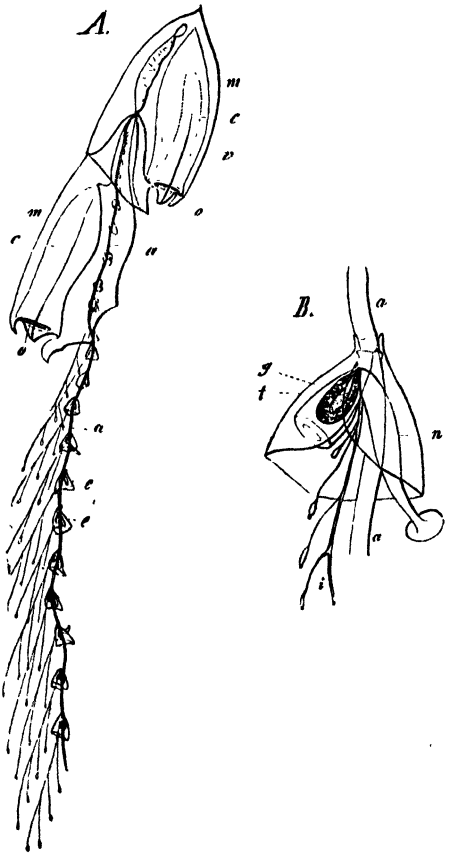

FIG. 58.—*Diphyes campanulata.*

A, the entire colony, natural size, showing stem (*a*) bearing groups of zooids (*e*) and two swimming bells (*m*, *m*), the apertures of which are marked *o*.

B, one of the groups of zooids marked *e* in A, showing common stem, (*a*), hydranth (*n*), medusoid (*g*), bract (*t*), and branched tentacle or grappling line (*i*). (From Gegenbaur.)

minal mouth, like the manubrium of a medusa, surrounded by a great number of structures like hollow tentacles (*hy'*).

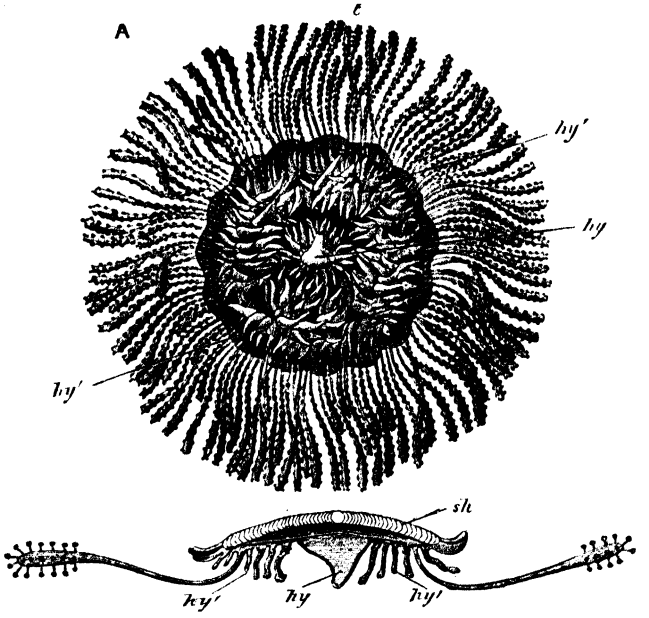

FIG. 59.—A, *Porpita pacifica* (nat. size), from beneath, showing disc-like stem surrounded by tentacles (*t*), a single functional hydranth (*hy*), and numerous mouthless hydranths (*hy'*).

B, vertical section of *P. mediterranea*, showing the relative positions of the functional (*hy*) and mouthless (*hy'*) hydranths, the tentacles, and the chambered shell (*sh*). (A after Duperrey; B from Huxley, after Kölliker.)

The discoid body is supported by a sort of shell having the consistency of cartilage and divided into chambers which contain air (B, *sh*).

Accurate examination shows that the manubrium-like

body (*hy*) on the under surface is a hydranth, that the short, hollow, tentacle-like bodies (*hy'*) surrounding it are mouthless hydranths, and that the disc represents the common stem of Diphyes or Bougainvillea. So that Porpita is not what it appears at first sight, a single individual, like a Medusa or a Hydra, but a colony in which the constituent zooids have become so modified in accordance with an extreme division of physiological labour, that the entire colony has the character of a single physiological individual.

It was pointed out in the previous lesson (p. 230) that Hydra, while morphologically the equivalent of an indefinite number of unicellular organisms, was yet physiologically a single individual, its constituent cells being so differentiated and combined as to form one whole. A further stage in this same process of individuation is seen in Porpita, in which not cells but zooids, each the morphological equivalent of an entire Hydra, are combined and differentiated so as to form a colony which, from the physiological point of view, has the characters of a single individual.

LESSON XXIII

SPERMATOGENESIS AND OOGENESIS. THE MATURATION AND IMPREGNATION OF THE OVUM. THE CONNECTION BETWEEN UNICELLULAR AND DIPLOBLASTIC ANIMALS

In the preceding lessons it has more than once been stated that sperms arise from ordinary undifferentiated cells in the spermary, and that ova are produced by the enlargement of similar cells in the ovary. Fertilisation has also been described as the conjugation or fusion of ovum and sperm. We have now to consider in greater detail what is known as to the precise mode of development of sperms (*spermatogenesis*) and of ova (*oogenesis*), as well as the exact steps of the process by which an oosperm or unicellular embryo is formed by the union of the two sexual elements. The following description applies to animals: recent researches show that essentially similar processes take place in plants.

Both ovary and spermary are at first composed of cells of the ordinary kind, the *primitive sex-cells*, and it is only by the further development of these that the sex of the gonad is determined.

In the spermary the sex-cells (Fig. 60, A) undergo repeated fission, forming what are known as the sperm-mother-cells (B). These have been found in several instances to be

distinguished by a peculiar condition of the nucleus. We saw (p. 65) that the number of chromosomes is constant in

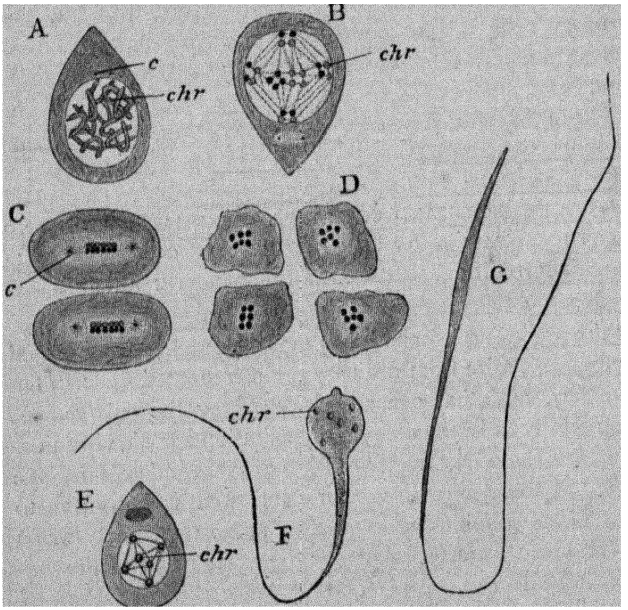

FIG. 60.—Spermatogenesis in the Mole-Cricket (*Gryllotalpa*).

A. Primitive sex-cell, just preparatory to division, showing twelve chromosomes (*chr*), *c*, the centrosome.

B. Sperm-mother-cell, formed by the division of A, and containing twenty-four chromosomes. The centrosome has divided into two.

C. The sperm-mother-cell has divided into two by a reducing division, each daughter-cell containing twelve chromosomes.

D. Each daughter-cell has divided again in the same manner, a group of four sperm-cells being produced, each with six chromosomes.

E. A single sperm-cell about to elongate to form a sperm.

F. Immature sperm; the six chromosomes are still visible in the head.

G. Fully formed sperm.

(After von Rath.)

any given animal, though varying greatly in different species. In the formation of the sperm-mother-cells from the primitive sex-cells the number becomes doubled: in the case of the mole-cricket, for instance, shown in Fig. 61, while the ordinary cells of the body, including the primitive sex-cells, contain twelves chromosomes, the sperm-mother-cells contain twenty-four.

The sperm-mother-cell now divides (C), but instead of its chromosomes splitting in the ordinary way (p. 64 and Fig. 10) half of their total number —in the present instance twelve— passes into each daughter cell: in this way two cells are produced having the normal number of chromosomes. The process of division is immediately repeated in the same peculiar way (D), the result being that each sperm-mother-cell gives rise to a group of four cells having half the normal number of chromosomes—in the present instance six. The four cells thus produced are the immature sperms (E): in the majority of cases the protoplasm of each undergoes a great elongation, being converted into a long vibratile thread, the *tail* of the sperm (F, G), while the nucleus becomes its more or less spindle-shaped *head* and the centrosome takes the form of a small *intermediate piece* at the junction of head and tail.

Thus the sperm or male gamete is a true cell, specially modified in most cases for active movement: its head, representing the nucleus, is directed forwards in progression, its long tail, formed from the protoplasm, backwards. The direction of movement is thus the precise opposite of that of a monad (p. 36) to which a sperm presents a certain resemblance. This actively motile tailed form is, however, by no means essential: in many animals the sperms are non-motile and in some they resemble ordinary cells.

The peculiar variety of mitosis described above, by which

the number of chromosomes in the sperm-mother-cells is reduced by one-half, is known as a *reducing division*.

As already stated, the ova arise from primitive sex-cells, precisely resembling those which give rise to sperms. These divide and give rise to the *egg-mother-cells* in which, as in the sperm-mother-cells, the number of chromosomes is doubled. The egg-mother-cells do not immediately undergo division but remain passive and increase, often enormously, in size, by the absorption of nutriment from surrounding parts: in this way each egg-mother-cell becomes an *ovum*. Sometimes this nutriment is simply taken in by osmosis, in other cases the growing ovum actually ingests neighbouring cells after the manner of an Amœba. Thus in the developing egg the processes of constructive are vastly in excess of those of destructive metabolism.

We saw in the second lesson (p. 33) that the products of destructive metabolism might take the form either of waste products which are got rid of, or of plastic products which are stored up as an integral part of the organism. In the developing egg, in addition to increase in the bulk of the protoplasm itself, a formation of plastic products usually goes on to an immense extent. In plants the stored-up materials may take the form of starch, as in Nitella (p. 214), of oil, or of proteid substance: in animals it consists of rounded or angular grains of proteid material, known as *yolk-granules*. These being deposited, like plums in a pudding, in the protoplasm, have the effect of rendering the fully-formed egg opaque, so that its structure can often be made out only in sections. When the quantity of yolk is very great the ovum may attain a comparatively enormous size, as for instance in birds, in which, as already mentioned (p. 69), the "yolk" is simply an immense egg-cell.

When fully formed, the typical animal ovum (Fig. 61)

consists of a more or less globular mass of protoplasm, generally exhibiting a reticular structure and enclosing a larger or smaller quantity of yolk-granules. Surrounding the cell-body is usually a cell-wall or cuticle, often of considerable thickness and known as the *vitelline membrane*: frequently it is perforated at one pole by an aperture, the *micropyle* (fig. 62, *microp*). The nucleus is large and has

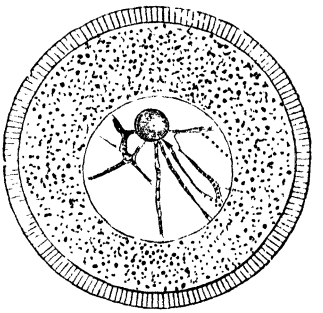

FIG. 61.—Ovum of a Sea-urchin (*Toxopneustes lividus*), showing the radially-striated cell-wall (vitelline membrane), the protoplasm containing yolk granules (vitellus), the large nucleus (germinal vesicle) with its network of chromatin, and a large nucleolus (germinal spot). (From Balfour after Hertwig.)

the usual constituents (p. 63)—nuclear membrane, nuclear sap, and chromatin. As a rule there is a very definite nucleolus, which is often known as the *germinal spot*, the entire nucleus being called the *germinal vesicle*.

Such a fully-formed ovum is, however, incapable of being fertilized or of developing into an embryo: before it is ripe for conjugation with a sperm or able to undergo the first stages of segmentation it has to go through a process known as the *maturation of the egg*.

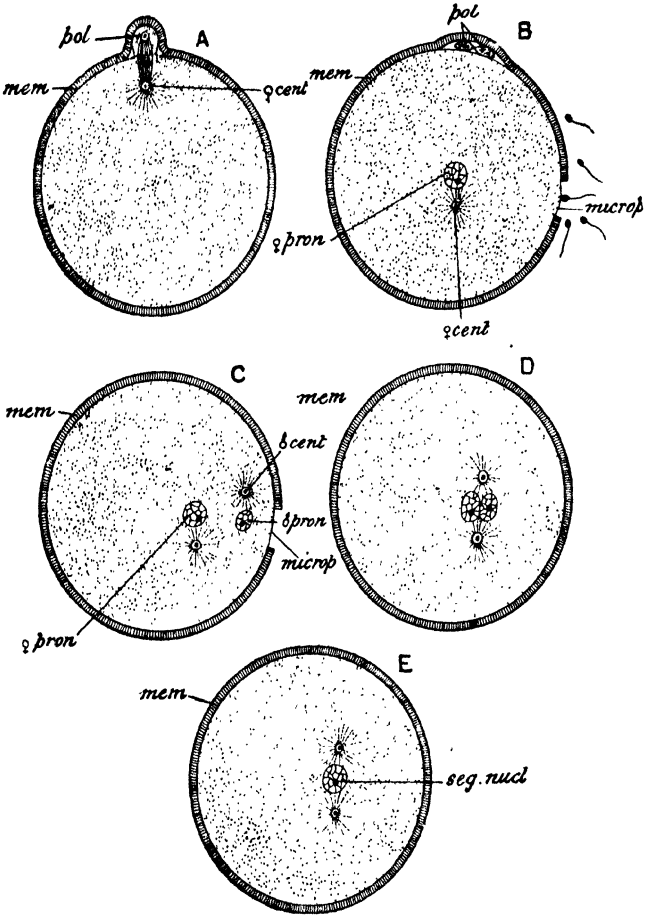

FIG. 62.—The Maturation and Impregnation of the Animal Ovum.

A, the ovum, surrounded by the vitelline membrane (*mem*), in the act of forming the first polar cell (*pol*) : ♀ *cent*, centrosome.

B, both polar cells (*pol*) are formed, the female pronucleus (♀ *pron*) lies near the centre of the ovum, and one of several sperms is shown making its way into the ovum at the micropyle (*microp*).

C, the head of the sperm has become the male pronucleus (♂ *pron*), its intermediate piece the male centrosome (♂ *cent*); other structures as before.

D, the male and female pronuclei are in the act of conjugation.

E, conjugation is complete and the segmentation nucleus (*segt. nucl*) formed. (From Parker and Haswell's *Zoology*.)

Maturation consists essentially in a twice-repeated process of cell-division. The nucleus (Fig. 62, A,) loses its membrane, travels to the surface of the egg, and takes on the form of an ordinary nuclear spindle. Next the protoplasm grows out into a small projection or bud, into which one end of the spindle projects. The usual process of nuclear division then takes place (Fig. 10, p. 64), one of the daughter nuclei remaining in the bud (*pol*), the other in the ovum itself. Nuclear division is followed as usual by division of the protoplasm, and the bud becomes separated as a small cell distinguished as the *first polar cell*.

It was mentioned in a previous lesson (p. 200) that in some cases development from an unfertilized female gamete took place, the process —which is not uncommon among insects and crustaceans —being distinguished as parthenogenesis. It has been proved in many instances and may be true in the majority of cases that the egg begins to develop after the formation of the first polar cell. Thus in many parthenogenetic ova maturation is completed by the separation of a single polar cell.

In the majority of animals, however, development takes place only after fertilization, and in such cases maturation is not complete until a *second polar cell* (B, *pol*) has been formed in the same manner as the first. The ovum has now lost a portion of its protoplasm together with three-fourths of its chromatin, half having passed into the first polar cell and half of what remained into the second: the remaining one-fourth of the chromatin takes on a rounded form and is distinguished as the *female pronucleus* (B, ♀ *pron*).

The formation of both polar cells takes place by a reducing division, so that, while the immature ovum contains double the number of chromosomes found in the ordinary cells of the species, the mature ovum, like the sperm, contains only one-half the normal number.

In some animals the first polar body has been found to divide after separating from the egg. In such cases the egg-mother-cell or immature ovum gives rise to a group of four cells—the mature ovum and three polar-cells; just as the sperm-mother-cell gives rise to a group of four cells, all of which, however, become sperms.

After maturation has taken place, the ovum is ready to be fertilized by the conjugation with it of a single sperm. As we have found repeatedly, sperms are produced in vastly greater numbers than ova, and it often happens that a single egg is seen quite surrounded with sperms, all apparently about to conjugate with it. It has however been found to be a general rule that only one of these actually conjugates: the others, like most drones in a hive, perish without fulfilling the one function they are fitted to perform.

The successful sperm (B) takes up a position at right angles to the surface of the egg, and gradually passes through the micropyle (*microp*) or works its way through the vitelline membrane until its head lies within the egg-protoplasm. The tail is then cast off and the head, accompanied by the intermediate piece or centrosome, penetrating deeper into the protoplasm, takes on the form of a rounded nucleus-like body, the *male pronucleus* (C, ♂ *pron*).

The two pronuclei approach one another (D) and finally unite to form what is called the *segmentation nucleus* (E, *seg. nucl*), the single nucleus of what is not now the *ovum* but the *oosperm*—the impregnated egg or unicellular embryo. The fertilizing process is thus seen to consist of the union

of two nuclear bodies, one contributed by the male gamete or sperm, the other by the female gamete or ovum. It follows from this that the essential nuclear matter or chromatin of the oosperm is derived in equal proportions from each of the two parents.

Moreover, as both male and female pronuclei contain only half the number of chromosomes found in the ordinary cells of the species, the union of the pronuclei results in the restoration of the normal number to the oosperm.

In some cases the astrospheres of the sperm and ovum as well as their nuclei appear to unite with one another, but more usually the egg-centrosome degenerates and disappears, the centrosome of the oosperm—and consequently of all the cells of the fully-formed animal—being derived from the centrosome of the sperm, *i.e.* from the male parent.

Fertilization being thus effected, the process of segmentation or division of the oosperm takes place as described in the preceding lesson (p. 246).

In concluding the present lesson, we shall consider briefly a point which has probably already struck the reader. Among the plant-forms which have come under our notice there has been a very complete series of gradations from the simple cell, through the non-cellular filament, linear aggregate, and superficial aggregate, to the solid aggregate, whilst among the animals already discussed there has so far been no attempt to fill up the very considerable gap between unicellular and multicellular forms. In Amœba, Vorticella, &c., the entire animal is a single cell, while our next animal type, Hydra, is not only a solid aggregate but has its cells arranged in two definite layers enclosing a digestive cavity. Moreover, in unicellular organisms repro

duction is effected either asexually by the fission of the entire individual, or in the case of sexual reproduction, follows after two entire individuals have undergone conjugation. In multicellular forms, on the other hand, single cells are set apart for sexual reproduction.

When we say that no attempt has been made to fill up this gap, we mean as far as adult forms are concerned. If the reader will turn to the account, in the previous lesson, of the development of hydroid polypes (p. 246), he will see that the facts there described do as a matter of fact help us to see a possible connection between unicellular animals and multicellular two-layered forms with mouth and digestive cavity. The oosperm of the hydroid (Fig. 57, A) has the essential character of an Amœba, the polyplast (E) is practically a colony of Amœbæ, and the planula (H) a similar colony in which the zooids (cells) are dimorphic, being arranged in two layers, with a central cavity which finally communicates with the exterior by a mouth.

It is an interesting circumstance that these embryonic stages are to some extent paralleled by certain adult organisms, two of the more accessible and well-known of which will now be described.

Pandorina (Fig. 63, A) is a colony consisting of sixteen unicellular zooids closely packed in a gelatinous case of a globular form. Each zooid resembles in general characters a motile Hæmatoccus or Euglena, having an ovoid cell-body coloured green by chlorophyll, a red pigment-spot, and two flagella, which protrude through the gelatinous wall of the colony, and by their action impart to it a rotatory movement.

In asexual reproduction each of the sixteen zooids divides and re-divides, forming at last a group of sixteen cells. In

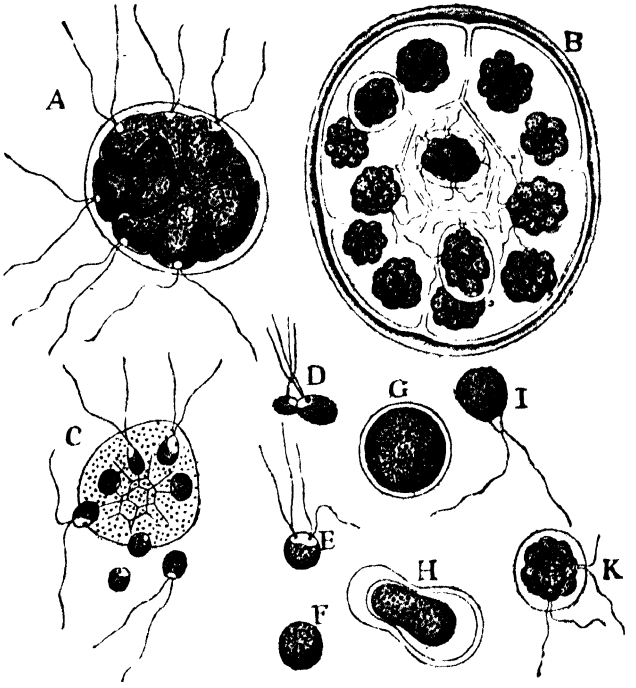

FIG. 63.—*Pandorina morum.*

A. The entire colony, consisting of sixteen flagellate zooids, enclosed in a gelatinous envelope.

B. Asexual reproduction ; each zooid has divided into sixteen, forming as many daughter families, still enclosed within the original gelatinous envelope.

C. Sexual reproduction ; zooids are being set free from the colony, forming gametes.

D. Conjugation of two gametes.

E. The same after complete fusion.

F. The immature zygote.

G. The fully-formed zygote.

H. Protoplasm of zygote escaping from cell-wall.

I. The same after acquisition of flagella.

K. The same undergoing division and forming a young colony. (From Goebel.)

this way sixteen daughter colonies are produced within the gelatinous envelope of the original mother colony (B). By the solution of the envelope the daughter colonies are set free, and each begins an independent existence.

In sexual reproduction the zooids are set free singly from the colony (C). They swim about actively, approach one another in pairs, and conjugate (D), becoming completely fused together (E) to form a zygote (F). This increases in size and develops a thick cell wall (G). After a period of rest, the protoplasm escapes from the cell wall (H), puts out a pair of flagella (I), and swims about. Finally it settles down, divides and re-divides, and so gives rise to a new colony (K).

It is obvious that Pandorina resembles the polyplast stage of an embryo: moreover it is produced by the repeated fission of a zygote, just as the polyplast is formed by the repeated fission of an oosperm.

The beautiful *Volvox* (Figs 64 and 65), one of the favourite studies of microscopists, is a colony of Hæmatococcus-like zooids arranged in the form of a hollow sphere containing a transparent mucilage. Each cell (C) has a nucleus, a contractile vacuole, a large green chromatophore, a small red pigment-spot like that of Euglena (p 47) and two flagella. The cells are surrounded by thick mucilaginous cell-walls which do not give the reaction of cellulose, but are probably formed of an allied carbohydrate. By the combined movement of all the flagella a rotating movement is given to the entire colony.

Asexual reproduction takes place by means of certain zooids distinguished from the rest by the absence of flagella, and called *parthenogonidia* (Fig. 64. A, *a*). Each parthenogonidium undergoes a process very like the segmentation of the hydroid egg (p. 246), dividing into 2, 4, 8, 16, &c. cells

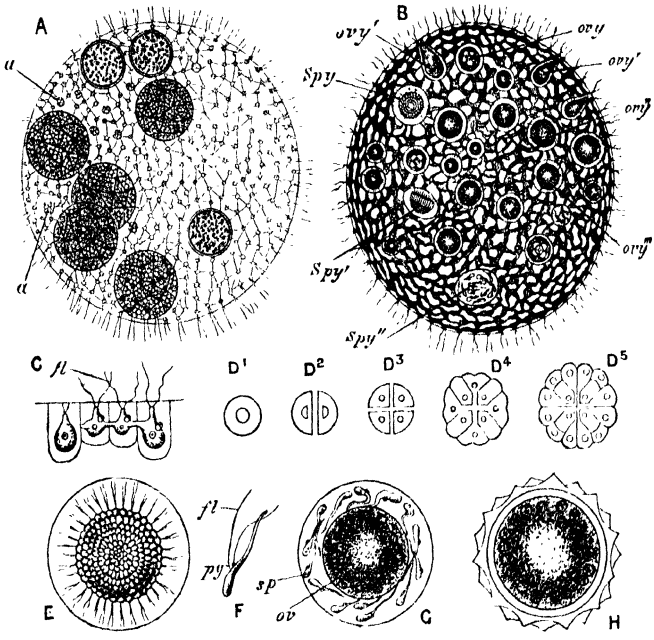

FIG. 64.—*Volvox globator.*

A, the entire colony, surface view, showing the biflagellate zooids and several daughter-colonies swimming freely in the interior; the latter are produced by the repeated fission of non-flagellate reproductive zooids or parthenogonidia (*a*)

B, the same during sexual maturity, showing spermaries from the surface (*spy*), in profile (*spy'*), and after complete formation of sperms (*spy''*): and ovaries from the surface (*ovy*, *ovy''*, *ovy'''*) and in profile (*ovy'*).

C, four zooids in optical section, showing cell-wall, nucleus, contractile vacuole, with adjacent pigment-spot, and flagella (*fl*).

D^1–D^5, stages in the formation of a colony by the repeated binary fission of an asexual reproductive zooid.

E, a ripe spermary.

F, a single sperm, showing pigment-spot (*pg*) and flagella (*fl*).

G, an ovary containing a single ovum surrounded by several sperms.

H, oosperm enclosed in its spinose cell-wall.

(A from Geddes and Thomson, after Kirchner; B-H after Cohn.)

(A, *a*, and D^1--D^5), and so forming a daughter colony which becomes detached and swims freely in the interior of the parent colony (A), by the rupture of which it is finally liberated. In sexual reproduction certain cells enlarge and take on the characters of ovaries (B, *ovy*, *ovy'*, *ovy''*, *ovy'''*, and Fig. 66, *o*) the protoplasm of each forming a single

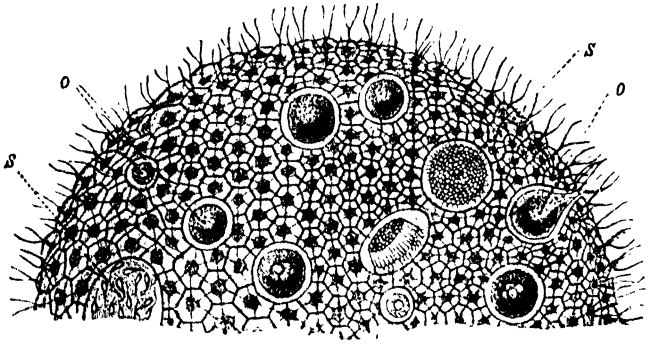

FIG. 65.

Part of a Volvox-colony showing the structure in greater detail than in Fig. 64: *s*, spermaries; *o*, ovaries. (From Lang.)

ovum: the protoplasm of others divides repeatedly and forms aggregations of sperms (B, *spy*, *spy'*, *spy''*, and Fig. 65, *s*). By the conjugation of a sperm (F) with an ovum (G) an oosperm (H) is produced, and from this by continued division a new colony arises.

Volvox is clearly comparable to a hollow polyplast, and further resembles the higher or multicellular animals in that certain of its cells are differentiated to form true sexual products.

It is necessary, in conclusion, to remind the reader that

the Mycetozoa and Opalina may be said to take an intermediate place between the strictly unicellular and the multicellular animals in much the same way as Mucor and Vaucheria connect unicellular and multicellular plants. The plasmodium of the Mycetozoa is formed, in the first instance (p. 54), by the fusion of amœbulæ: hence it is a many-celled structure, the constituent cells of which have lost their boundaries and are indicated only by their nuclei. Subsequently the nuclei multiply by division, and, although the process does not affect the protoplasm, it is allowable to say that the number of virtual cells of which the plasmodium is composed is thereby increased. The Mycetozoon, in its plasmodial stage, is, in fact, a non-cellular organism, like Mucor or Vaucheria. But if this way of looking at the Mycetozoa is correct, it follows that Opalina is to be considered rather as a multinucleate but non-cellular than as a unicellular animal.

LESSON XXIV

POLYGORDIUS

POLYGORDIUS is a minute worm, about 3 or 4 cm. in length, found in the European seas, where it lives in sand at a depth of a few fathoms. It has much the appearance of a tangle of pink thread with one end produced into two delicate processes (Fig. 66, A). These, which are the *tentacles*, mark the anterior end of the animal—the opposite extremity, which in some species also bears a pair of slender processes, is the posterior end. As the creature creeps along, one side is kept constantly upwards and is distinguished as the dorsal aspect; the lower surface is called ventral.

The anterior end is narrower than the rest of the body, and is marked off behind by a groove (B and C); this division is called the *prostomium* (*Pr. st*) and bears the tentacles (*t*) already mentioned in front and above, and on each side a small oval depression (*c. p*) lined with cilia. Immediately following the prostomium is a region clearly marked off in front, but ill-defined posteriorly, and known as the *peristomium* (*Per. st*); on its ventral surface is a transverse triangular aperture the mouth (*Mth*). The rest of the body is more or less distinctly marked by annular grooves (D and E, *gr*) into *body-segments* or *metameres*

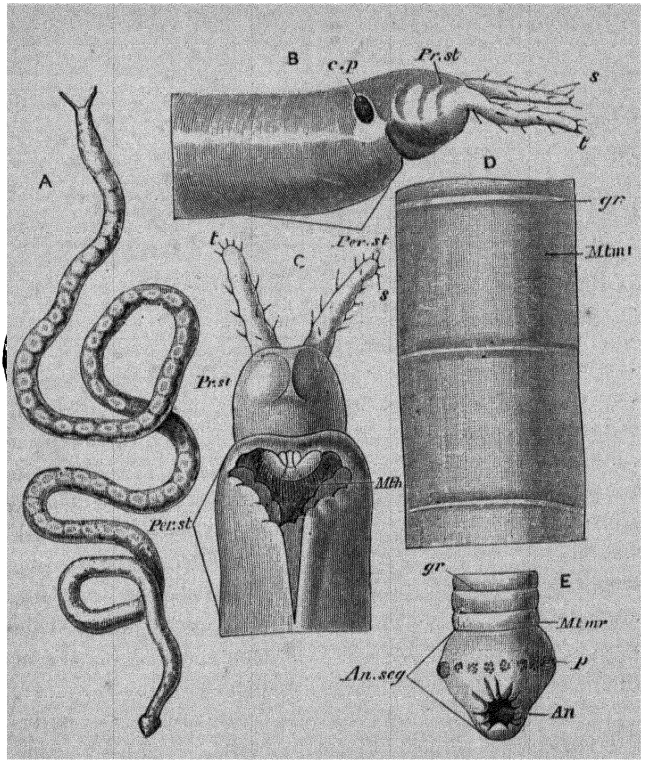

FIG. 66.—*Polygordius neapolitanus.*

A, the living animal, dorsal aspect, about five times natural size.

B, anterior end of the worm from the right side, more highly magnified, showing the prostomium (*Pr. st*), peristomium (*Per. st*), tentacles (*t*), with setæ (*s*) and ciliated pit (*c. p*).

C, ventral aspect of the same : letters as before except *Mth*, mouth.

D, portion of body showing metameres (*Mtmr*) separated by grooves (*gr*).

E, posterior extremity from the ventral aspect, showing the last three metameres (*Mtmr*) separated by distinct grooves (*gr*), the anal segment (*An. seg*) bearing the anus (*An*), and a circlet of papillæ (*p*). (After Fraipont.)

(*Mtmr*), the number of which varies considerably. Polygordius is thus the first instance we have met with of a transversely segmented animal. The last or *anal segment* (E, *An. seg*) differs from the others by its swollen form and by bearing a circlet of little prominences or papillæ (*p*); it is separated from the preceding segment by a deep groove and bears at its posterior end a small circular aperture, the anus (*An*).

Polygordius may therefore be described as consisting of a number of more or less distinct *segments* which follow one another in longitudinal series; three of these, the *prostomium*, which lies altogether in front of the mouth, the *peristomium*, which contains the mouth, and the *anal segment*, which contains the anus, are constant and are distinguished by special characters; while between the peristomium and the anal segment are intercalated a variable number of *metameres* which resemble one another in all essential respects.

Polygordius feeds in much the same way as an earthworm: it takes in sand, together with the various nutrient matters contained in it, such as infusoria, diatoms, &c., by the mouth, and after retaining it for a longer or shorter time in the body, expels it by the anus. It is obvious, therefore, that there must be some kind of digestive cavity into which the food passes by the mouth, and from which effete matters are expelled through the anus. Sections (Fig. 67) show that this cavity is not a mere space excavated in the interior of the body, but a definite tube, the *enteric canal* (A, B), which passes in a straight line from mouth to anus, and is separated in its whole extent from the walls of the body (A, *B. W*) by a wide space, the *body cavity* or *cœlome* (*Cœl*). So that the general structure of Polygordius might be imitated by taking a wide tube, stopping the ends of it with

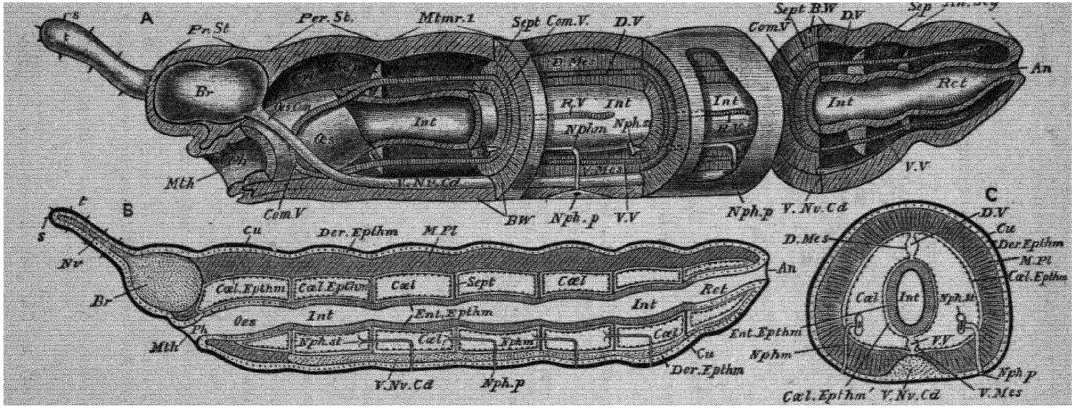

FIG. 67.[1]—A, semi-diagrammatic figure of the anatomy of Polygordius in the form of a dissection from the left side.

The prostomium (*Pr. st*), peristomium (*Per. st*), and first three metameres (*Mtmr.* 1, &c.) are shown to the left, the last two metameres and the anal segment (*An. seg*) to the right; the remaining metameres are supposed to be removed; the right tentac[illegible] is shown with its setæ (*s*).

The body-wa[illegible]. *B*) is shown mainly in longitudinal section, but, in the anterior metameres, part of it is seen from the surface and [illegible] in transverse section.

The mouth [illegible] leads into the enteric canal, which is somewhat dilated in each segment, and ends posteriorly in the anus (*An*); it is shown partly entire, partly in section: *Ph*, pharynx; *Oes*, oesophagus; *Int*, intestine; *Rct*, rectum.

[1] The diagrammatic figures in this and the following illustrations to Polygordius are founded upon Fraipont's figures, although not actually copied from them.

Between the enteric canal and the body-wall is the cœlome (*Cœl*), divided into right and left portions by the dorsal (*D. Mes*) and ventral (*V. Mes*) mesenteries, and into segmental compartments by the septa (*Sept*).

Lying in the mesenteries are the dorsal (*D. V*) and ventral (*V. V*) blood-vessels, connected by commissural vessels (*Com. V*) running in the septa: from the latter go off recurrent vessels (*R. V*).

Nephridia (*Nphm*) are shown in the second and third metameres, each consisting of a horizontal portion which perforates a septum and opens in the preceding segment by a nephrostome (*Nph. st*) and of a vertical portion which perforates the body-wall and opens externally by a nephridiopore (*Nph. p*).

The brain (*Br*) lies in the prostomium and is connected with the ventral-nerve cord (*V. Nv. Cd.*) by a pair of œsophageal connectives (*Œs. Com*).

B, diagrammatic longitudinal section showing the cell-layers.

The cuticle is represented by a black line, the ectoderm is dotted, the endoderm radially striated, the muscle plates evenly shaded, the cœlomic epithelium represented by a beaded line, and the nervous system finely dotted.

The body-wall is composed of cuticle (*Cu*), deric epithelium (*Der. Epthm*), muscle-plates (*M. Pl*), and parietal layer of cœlomic epithelium (*Cœl. Epthm*).

The enteric canal is formed of enteric epithelium (*Ent. Epthm*) covered by the visceral layer of cœlomic epithelium (*Cœl. Epthm'*); in the neighbourhood of the mouth (*Mth*) and anus (*An*) the enteric epithelium is ectodermal; elsewhere it is endodermal; *Ph*, pharynx; *Oes*, œsophagus; *Int*, intestine; *Rct*, rectum.

The septa (*Sept*) are formed of muscle covered on both sides by cœlomic epithelium.

Four nephridia (*Nphm*) with nephrostome (*Nph. st*) and nephridiopore (*Nph. p*) are shown.

The brain (*Br*) and ventral nerve cord (*V. Nv. Cd*) are seen to be in contact with the ectoderm: from the brain a nerve (*nv*) passes to the tentacle.

C, diagrammatic transverse section showing the cell-layers as in B, viz. the cuticle (*Cu*), deric epithelium (*Der. Epthm*), muscle-plates (*M. Pl*), and parietal layer of cœlomic epithelium (*Cœl. Epthm*), forming the body-wall; and the enteric epithelium (*Ent. Epthm*) and visceral layer of cœlomic epithelium (*Cœl. Epthm'*), forming the enteric canal.

The dorsal (*D. Mes*) and ventral (*V. Mes*) mesenteries are seen to be formed of a double layer of cœlomic epithelium, and to enclose respectively the dorsal (*D. V*) and ventral (*V. V*) blood-vessels.

A nephridium (*Nphm*) is shown on each side with nephrostome (*Nph. st*) and nephridiopore (*Nph. p*).

The connection of the ventral nerve-cord with the ectoderm (deric epithelium) is well shown.

Fig. 70, A (p. 291), should be compared with this figure, as it is an accurate representation of the parts shown here diagrammatically.

corks, boring a hole in each cork, and then inserting through the holes a narrow tube of the same length as the wide one. The outer tube would represent the body-wall, the inner the enteric canal, and the cylindrical space between the two the cœlome. The inner tube would communicate with the exterior by each of its ends, representing respectively mouth and anus; the space between the two tubes, on the other hand, would have no communication with the outside.

Polygordius is the first example we have studied of a *cœlomate* animal: one in which there is a definite body-cavity separating from one another the body-wall and the enteric canal, and in which therefore a transverse section of the body has the general character of two concentric circles (Fig. 67, c).

It will be remembered that a transverse section of Hydra has the character of two concentric circles, formed respectively of ectoderm and endoderm (Fig. 56, A′, p. 241), the two layers being, however, in contact or separated only by the thin mesoglœa. At first sight then, it seems as if we might compare Polygordius to a Hydra in which the ectoderm and endoderm instead of being in contact were separated by a wide interval; we should then compare the body-wall of Polygordius with the ectoderm of Hydra and its enteric canal with the endoderm. But this comparison would only express part of the truth.

A thin transverse section shows the body-wall of Polygordius to consist of four distinct layers. Outside is a thin transparent cuticle (Fig. 67, c, and Fig. 70, A, *cu*) showing no structure beyond a delicate striation. Next comes a layer of epithelium (*Der. Epthm*), showing no cell-boundaries and thus having the character of a sheet of protoplasm with regularly disposed nuclei: this is the *deric epithelium* or *epidermis*. Within it is a rather thick layer of *muscle-plates*

(*M. Pl*), having the form of long flat spindles (Fig. 69, p. 284, *M. Pl.*) exhibiting a delicate longitudinal striation and covered on their free services with a fine network of protoplasm containing scattered nuclei. Each plate is arranged longitudinally, extending through several segments, and with its short axis perpendicular to the surface of the body (Fig. 70, *M. Pl.*). It is by the contraction of the muscle-plates that the movements of the body, which resemble those of an earthworm, are produced. Finally, within the muscular layer and lining the cœlome is a very thin layer of cells, the *cœlomic epithelium* (*Cœl. Epthm*).

A transverse section of the enteric canal shows only two layers. The inner consists of elongated cells (*Ent. Epthm*) fringed on their inner or free surfaces with cilia: these constitute the *enteric epithelium*. Outside these is a very thin layer of flattened cells (*Cœl. Epthm'*) bounding the cœlome, and hence called, like the innermost layer of the body-wall, cœlomic epithelium. We have, therefore, to distinguish two layers of cœlomic epithelium, an outer or *parietal layer* (*Cœl. Epthm.*) which lines the body-wall, and an inner or *visceral layer* (*Cœl. Epthm'*) which invests the enteric canal

We are now in a better position to compare the transverse sections of Hydra and of Polygordius (Fig. 55, A', and Fig. 67, C). The deric epithelium of Polygordius being the outermost cell-layer is to be compared with the ectoderm of Hydra, and its cuticle with the layer of the same name which, though absent in Hydra, is present in the stem of hydroid polypes such as Bougainvillea (p. 238). The enteric epithelium of Polygordius, bounding as it does the digestive cavity, is clearly comparable with the endoderm of Hydra. So that we have the layer of muscle-plates and the two layers of cœlomic epithelium not represented in Hydra, in which their position is occupied merely by the mesoglœa.

But it will be remembered that in polypes there is sometimes found a layer of separate muscle-fibres between the ectoderm and the mesoglœa, and it was pointed out (p. 236) that such fibres represented a rudimentary intermediate cell-layer or mesoderm. We may therefore consider the muscular layer and the cœlomic epithelium of Polygordius as mesoderm, and we may say that in this animal the mesoderm is divisible into an outer or *somatic layer*, consisting of the muscle-plates and the parietal layer of cœlomic epithelium, and an inner or *splanchnic layer*, consisting of the visceral layer of cœlomic epithelium.[1]

The somatic layer is in contact with the ectoderm or deric epithelium, and with it forms the body-wall; the splanchnic layer is in contact with the endoderm or enteric epithelium and with it forms the enteric canal. The cœlome separates the somatic and splanchnic layers from one another, and is lined throughout by cœlomic epithelium.

The relation between the diploblastic polype and the triploblastic worm may therefore be expressed in a tabular form as follows—

Hydroid	*Polygordius.*	
Cuticle	Cuticle.	
Ectoderm	Deric epithelium or epidermis.	
Mesoderm (rudimentary)	Somatic layer	Muscle-plates.
		Cœlomic epithelium (parietal layer).
	Splanchnic layer	Cœlomic epithelium (visceral layer).
Endoderm	Enteric epithelium.	

[1] In the majority of the higher animals there is a layer of muscle between the enteric and cœlomic epithelia: in such cases the body-wall and enteric canal consist of the same layers but in reverse order, the cœlomic epithelium being internal in the one, external in the other.

Strictly speaking, this comparison does not hold good of the anterior and posterior ends of the worm: at both mouth and anus the deric passes insensibly into the enteric epithelium, and the study of development shows (p. 296) that the cells lining both the anterior and posterior ends of the canal are, as indicated in the diagram (Fig. 67, B), ectodermal. For this reason the terms deric and enteric epithelium are not mere synonyms of ectoderm and endoderm respectively.

It is important that the student should, before reading further, understand clearly the general composition of a triploblastic animal as typified by Polygordius, which may be summarised as follows. It consists of two tubes formed of epithelial cells, one within and parallel to the other, the two being continuous at either end of the body where the inner tube (enteric epithelium) is in free communication with the exterior; the outer tube (deric epithelium) is lined by a layer of muscle-plates within which is a thin layer of cœlomic epithelium, the three together forming the body-wall; the inner tube (enteric epithelium) is covered externally by a layer of cœlomic epithelium which forms with it the enteric canal; lastly, the body-wall and enteric canal are separated by a considerable space, the cœlome.

The enteric canal is not, as might be supposed from the foregoing description, connected with the body-wall only at the mouth and anus, but is supported in a peculiar and somewhat complicated way. In the first place there are thin vertical plates, the *dorsal* and *ventral mesenteries* (Fig. 67, A and C, *D. Mes*, *V. Mes*), which extend longitudinally from the dorsal and ventral surfaces of the canal to the body wall, dividing the cœlome into right and left halves. The structure of the mesenteries is seen in a transverse section (Fig. 67, C, and Fig. 70, A) which shows that at the middle

dorsal line the parietal layer of cœlomic epithelium becomes deflected downwards, forming a two-layered membrane, the dorsal mesentery; the two layers of this on reaching the enteric canal diverge and pass one on either side of it, forming the visceral layer of cœlomic epithelium; uniting again below the canal, they are continued downwards as the ventral mesentery, and on reaching the body-wall diverge once more to join the parietal layer. Thus the mesenteries are simply formed of a double layer of cœlomic epithelium, continuous on the one hand with the parietal and on the other with the visceral layer of that membrane.

Beside the mesenteries, the canal is supported by transverse vertical partitions or *septa* (Fig. 67, A and B, *Sept*) which extend right across the body-cavity, each being perforated by the canal. The septa are regularly arranged and correspond with the external grooves by which the body is divided into metameres. Thus the transverse or metameric segmentation affects the cœlome as well as the body-wall. Each septum is composed of a sheet of muscle covered on both sides with cœlomic epithelium (B, *Sept*).

Where the septa come in contact with the enteric canal, the latter is more or less definitely constricted, so as to present a beaded appearance (A and B); thus we have segmentation of the canal as well as of the body-wall and cœlome.

The digestive canal, moreover, is not a simple tube of even calibre throughout, but is divisible into four portions. The first or *pharynx* (*Ph*) is very short, and can be protruded during feeding; the second, called the gullet or *œsophagus* (*Oes*), is confined to the peristomium and is distinguished by its thick walls and comparatively great diameter; the third or *intestine* (*Int*) extends from the first metamere to the last—*i.e.*, from the segment immediately following the peristomium to that immediately preceding the anal

segment; it is laterally compressed so as to have an elongated form in cross section (C, and Fig. 70, A): the fourth portion or *rectum* (*Rct*) is confined to the anal segment; it is somewhat dilated and is not laterally compressed. The epithelium of the intestine is, as indicated in the diagram (B), endodermal; that of the remaining divisions of the canal is ectodermal. The large majority of the cells in all parts of the canal are ciliated.

The cells of the enteric canal and especially those of the gullet are very granular, and like the endoderm cells of the hypostome of Hydra (p. 228) are to be considered as gland-cells. They doubtless secrete a digestive juice which, mixing with the various substances taken in by the mouth, dissolves the proteids and other digestible parts, so as to allow of their absorption. There is no evidence of intracellular digestion such as occurs in Hydra (p. 229), and it is very probable that the process is purely extra-cellular or enteric, the food being dissolved and rendered diffusible entirely in the cavity of the canal. By the movements of the canal—caused partly by the general movements of the body and partly by the contraction of the muscles of the septa, aided by the action of the cilia—the contents are gradually forced backwards and the sand and other indigestible matters are expelled at the anus.

The cœlome is filled with a colourless, transparent *cœlomic fluid* in which are suspended minute, irregular, colourless bodies, as well as oval bodies containing yellow granules. From the analogy of the higher animals one would expect these to be leucocytes (p. 56), but their cellular nature has not been proved.

The function of the cœlomic fluid is probably to distribute the digested food in the enteric canal to all parts of the

body. In Hydra, where the lining wall of the digestive cavity is in direct contact with the simple wall of the body the products of digestion can pass at once by diffusion from endoderm to ectoderm, but in the present case a means of communication is wanted between the enteric epithelium and the comparatively complex and distant body-wall. The peptones and other products of digestion diffuse through the enteric epithelium into the cœlomic fluid, and by the continual movement of the latter—due to the contractions of the body-wall—are distributed to all parts. Thus the external epithelium and the muscles, as well as the nervous system and reproductive organs, not yet described, are wholly dependent upon the enteric epithelium for their supply of nutriment.

We have now to deal with structures which we find for the first time in Polygordius, namely blood-vessels. Lying in the thickness of the dorsal mesentery is a delicate tube (Fig. 67, A and C, D.V.) passing along almost the whole length of the body: this is the *dorsal vessel*. A similar *ventral vessel* (V.V) is contained in the ventral mesentery,[1] and the two are placed in communication with one another in every segment by a pair of *commissural vessels* (A, *Com.v*) which spring right and left from the dorsal trunk, pass downwards in or close behind the corresponding septum, following the contour of body-wall, and finally open into the ventral vessel. Each commissural vessel, at about the middle of its length, gives off a *recurrent vessel* (R.V.) which passes backwards and

[1] The statement that the dorsal and ventral vessels lie in the thickness of the mesenteries requires qualification. As a matter of fact, these vessels are simply spaces formed by the divergence of the two layers of epithelium composing the mesentery (Fig. 67, C, and Fig. 70, A): only their anterior ends have proper walls.

ends blindly. The anterior parts of the commissural vessels lie in the peristomium and have an oblique direction, one on each side of the gullet. The whole of these vessels form a single, closed vascular system, there being no communication between them and any of the remaining cavities of the body.

The vascular system contains a fluid, the *blood*, which varies in colour in the different species of Polygordius, being either colourless, red, green, or yellow. In one species corpuscles (? leucocytes) have been found in it.

The function of the blood has not been actually proved in Polygordius, but is well known in other worms. In the common earthworm, for instance, the blood is red, the colour being due to the same pigment, *hæmoglobin*, which occurs in our own blood and in that of other vertebrate animals.

Hæmoglobin is a nitrogenous compound, containing, in addition to carbon, hydrogen, nitrogen, oxygen, and sulphur, a minute quantity of iron. It can be obtained pure in the form of crystals which are soluble in water. Its most striking and physiologically its most important property is its power of entering into a loose chemical combination with oxygen. If a solution of hæmoglobin is brought into contact with oxygen it acquires a bright scarlet colour, and the solution is then found to have a characteristic spectrum distinguished by two absorption-bands, one in the yellow, another in the green. Loss of oxygen changes the colour from scarlet to purple, and the spectrum then presents a single broad absorption-band intermediate in position between the two of the oxygenated solution.

This property is of use in the following way. All parts of the organism are constantly undergoing destructive metabolism and giving off carbon dioxide: this gas is absorbed by the blood, and at the same time the hæmoglobin gives up

its oxygen to the tissues. On the other hand, whenever the blood is brought sufficiently near the external air—or water in the case of an aquatic animal—the opposite process takes place, oxygen being absorbed and carbon dioxide given off. Hæmoglobin is therefore to be looked upon as a respiratory or oxygen-carrying pigment; its function is to provide the various parts of the body with a constant supply of oxygen, while the carbon dioxide formed by their oxidation is given up to the blood. The particular part of the body in which the carbon dioxide accumulated in the blood is exchanged for the oxygen of the surrounding medium is called a respiratory organ; in Polygordius, as in the earthworm and many other of the lower animals, there is no specialised respiratory organ—lung or gill—but the necessary exchange of gases is performed by the entire surface of the body.

In discussing in a previous lesson the differences between plants and animals, we found (p. 178) that in the unicellular organisms previously studied, the presence of an excretory organ in the form of a contractile vacuole was a characteristic feature of such undoubted animals as the ciliate Infusoria, but was absent in such undoubted plants as Vaucheria and Mucor. But the reader will have noticed that Hydra and its allies have no specialised excretory organ, waste products being apparently discharged from any part of the surface. In Polygordius we meet once more with an animal in which excretory organs are present, although, in correspondence with the complexity of the animal itself, they are very different from the simple contractile vacuoles of Paramœcium or Vorticella.

The excretory organs of Polygordius consist of little tubes called *nephridia*, of which each metamere possesses a pair, one on either side (Fig. 67, A, B, and C, *Nphm*). Each

nephridium (Fig. 68) is an extremely delicate tube consisting of two divisions bent at right angles. The outer division is placed vertically, lies in the thickness of the body-wall, and opens externally by a minute aperture, the *nephridiopore* (Figs. 67 and 68, *Nph. p*). The inner division is horizontal and lies in the cœlomic epithelium, passing forward it pierces the septum which bounds the segment in front (Fig. 67, A and B), and then dilates into a funnel-shaped extremity or *nephrostome* (*Nph. st*), which places its cavity in free communication with the cœlome. The whole interior of the tube as well as the inner face of the nephrostome is lined with cilia which work outwards.

FIG. 68.—A nephridium of Polygordius, showing the cilia lining the tube, the ciliated funnel or nephrostome (*Nph. st*), and the external aperture or nephridiopore (*Nph. p*). (After Fraipont.)

A nephridium may therefore be defined as a ciliated tube, lying in the thickness of the body-wall and opening at one end into the cœlome and at the other on the exterior of the body.

In the higher worms, such as the earthworm, the nephridia are lined in part by gland-cells, and are abundantly supplied with blood-vessels. Water and nitrogenous waste from all parts of the body pass by diffusion into the blood and are conveyed to the nephridia, the gland-cells of which withdraw the waste products and pass them into the cavities of the tubes, whence they are finally discharged into the surrounding medium. In all probability some such process as this takes place in Polygordius.

In discussing the hydroid polypes we found that one of the most important points of difference between the locomotive medusa and the fixed hydranth was the presence in the former of a well-developed nervous system (p. 243) consisting of an arrangement of peculiarly modified cells, to which the function of automatism was assigned. It is natural to expect in such an active and otherwise highly-organised animal as Polygordius a nervous system of a considerably higher degree of complexity than that of a medusa.

The central nervous system consists of two parts, the *brain* and the *ventral nerve-cord*. The brain (Fig. 67, A and B, *Br.*) is a rounded mass occupying the whole interior of the prostomium and divided by a transverse groove into two lobes, the anterior of which is again marked by a longitudinal groove. The ventral nerve-cord (*V. Nv. Cd.*) is a longitudinal band extending along the whole middle ventral line of the body from the peristomium to the anal segment. The posterior lobe of the brain is connected with the anterior end of the ventral nerve-cord by a pair of nervous bands, the *œsophageal connectives* (*Œs. Con.*) which pass respectively right and left of the gullet.

It is to be noted that one division of the central nervous system—the brain—lies altogether above and in front of the enteric canal, the other division—the ventral nerve-cord—altogether beneath it, and that, in virtue of the union of the two divisions by the œsophageal connectives, the enteric canal perforates the nervous system.

It is also important to notice that the nervous system is throughout in direct contact with the epidermis or ectoderm, the ventral cord appearing in sections (Fig. 67, C, and Fig. 70, A) as a mere thickening of the latter.

Both brain and cord are composed of delicate nerve-fibres

(Fig. 69, *Nv. F.*) interspersed with nerve-cells (*Nv. C*). In the cord the fibres are arranged longitudinally, and the nerve-cells are ventral in position, forming a layer in imme-

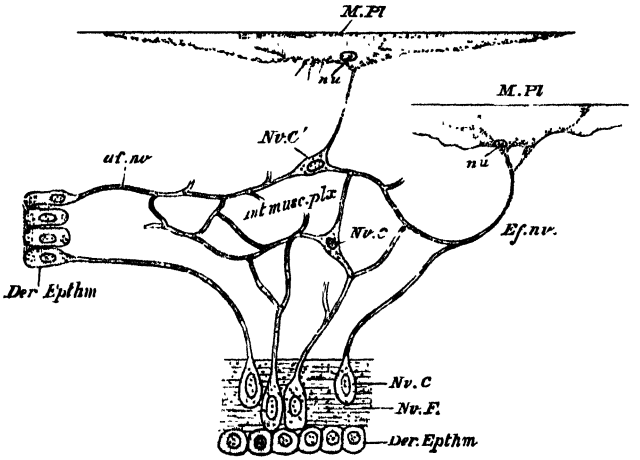

FIG. 69.—Diagram illustrating the relations of the nervous system of Polygordius.

The deric epithelium (*Der. Epthm*) is either in direct contact with the central nervous system (lower part of figure), or is connected by afferent nerves (*af. nv*) with the inter-muscular plexus (*int. musc. plx*): the latter is connected with the muscle-plates (*M. Pl*) by efferent nerves (*Ef. nv*).

The central nervous system consists of nerve-fibres (*Nv. F*) and nerve-cells (*Nv. C*): other nerve cells (*Nv. C'*) occur at intervals in the inter-muscular plexus.

The muscle-plates (*M. Pl*), one of which is entire, while only the middle part of the other is shown, are invested by a delicate protoplasmic network, containing nuclei (*nu*), to which the efferent nerves can be traced. (The details copied from Fraipont.)

diate contact with the deric epithelium. In the posterior lobe of the brain the nerve-cells are superficial and the central part of the organ is formed of a finely punctate

substance in which neither cells nor fibres can be made out.

Ramifying through the entire muscular layer of the body-wall is a network of delicate nerve-fibres (*int. musc. plx.*) with nerve-cells (*Nv. C'*) at intervals, the *inter-muscular plexus*. Some of the branches of this plexus are traceable to nerve-cells in the central nervous system, others (*af. nv.*) to epidermic cells, others (*Ef. nv.*) to the delicate protoplasmic layer covering the muscle-plates. The superficial cells of both brain and cord are also, as has been said, in direct connection with the overlying epidermis, and from the anterior end of the brain a bundle of nerve-fibres (Fig 67, B, *Nv.*) is given off on each side to the corresponding tentacle, constituting the *nerve* of that organ, to the epidermic cells of which its fibres are distributed.

We see then that, apart from the direct connection of nerve-cells with the epidermis, the central nervous system is connected, through the intermediation of nerve-fibres (*a*) with the sensitive cells of the deric epithelium and (*b*) with the contractile muscle-plates. And we can thus distinguish two sets of nerve-fibres, (*a*) *sensory* or *afferent* (*af. nv.*) which connect the central nervous system with the epidermis, and (*b*) *motor* or *efferent* (*Ef. nv.*) which connect it with the muscles.

Comparing the nervous system of Polygordius with that of a medusa (p. 243) there are two chief points to be noticed. Firstly, the concentration of the central nervous system in the higher type, and the special concentration at the anterior end of the body to form a brain. Secondly, the important fact that the inter-muscular plexus is not, like the peripheral nervous system of a medusa which it resembles, situated immediately beneath the epidermis (ectoderm) but lies in the muscular layer, or, in other words, has sunk into the mesoderm.

It is obvious that direct experiments on the nervous system would be a very difficult matter in so small an animal as Polygordius. But numerous experiments on a large number of other animals, both higher and lower, allow us to infer with considerable confidence the functions of the various parts in this particular case.

If a muscle be laid bare or removed from the body in a living animal it may be made to contract by the application of various stimuli, such as a smart tap (mechanical stimulus), a drop of acid or alkali (chemical stimulus), a hot wire (thermal stimulus), or an electric current (electrical stimulus). If the motor nerve of the muscle is left intact the application to it of any of these stimuli produces the same effect as its direct application to the muscle, the stimulus being conducted along the eminently irritable but non-contractile nerve.

Further, if the motor nerve is left in connection with the central nervous system, *i.e.*, with one or more nerve-cells, direct stimulation of these is followed by a contraction, and not only so, but stimulation of a sensory nerve connected with such cells produces a similar result. And finally, stimulation of an ectoderm cell connected, either directly or through the intermediation of a sensory nerve, with the nerve-cells, is also followed by muscular contraction. An action of this kind, in which a stimulus applied to the free sensitive surface of the body is transmitted along a sensory nerve to a nerve-cell or group of such cells and is then, as it were, reflected along a motor nerve to a muscle, is called a *reflex action;* the essence of the arrangement is the interposition of nerve-cells between sensory or afferent nerves connected with sensory cells, and motor or efferent nerves connected with muscles.

The diagram (Fig. 69) serves to illustrate this matter. The muscle-plate (*M. Pl.*) may be made to contract by a

stimulus applied (*a*) to itself directly, (*b*) to the motor fibre (*Ef. nv*), (*c*) to the nerve-cells (*Nv. C'*) in the central nervous system, or to those (*Nv. C'*) in the inter-muscular plexus, (*d*) to the sensory fibre (*af. nv.*), or (*e*) to the epidermic cells (*Der. Epthm*).

In all probability the whole central nervous system of Polygordius is capable of automatic action. It is a well-known fact that if the body of an earthworm is cut into several pieces each performs independent movements; in other words, the whole body is not, as in the higher animals, paralysed by removal of the brain. There can, however, be little doubt that complete co-ordination, *i.e.*, the regulation of the various movements to a common end, is lost when the brain is removed.

The nervous system is thus an all-important means of communication between the various parts of the organism and between the organism and the external world. The outer or sensory surface is by its means brought into connection with the entire muscular system with such perfection that the slightest touch applied to one end of the body may be followed by the almost instantaneous contraction of muscles at the other.

In some species of Polygordius the prostomium bears a pair of eye-specks, but in the majority of species the adult animal is eyeless, and, save for the ciliated pits (Fig. 66, B, *c.p*), the function of which is not known, the only definite organs of sense are the tentacles, which have a tactile function, their abundant nerve-supply indicating that their delicacy as organs of touch far surpasses that of the general surface of the body. They are beset with short, fine processes of the cuticle called *setæ* (Figs. 66 and 67, *s*), which probably, like the whiskers of a cat, serve as conductors of external stimuli to the sensitive epidermic cells.

There are two matters of general importance in connection with the structure of Polygordius to which the student's attention must be drawn in concluding the present lesson.

Notice in the first place how in this type, far more than in any of those previously considered, we have certain definite parts of the body set apart as *organs* for the performance of particular functions. There is a mouth for the reception of food, an enteric canal for its digestion, and an anus for the extrusion of fæces: a cœlomic fluid for the transport of the products of digestion to the more distant parts of the body: a system of blood-vessels for the transport of oxygen to and of carbon dioxide from all parts: an epidermis as organ of touch and of respiration: nephridia for getting rid of water and nitrogenous waste: and a definite nervous system for regulating the movements of the various parts and forming a means of communication between the organism and the external world. It is clear that differentiation of structure and division of physiological labour play a far more obvious and important part than in any of the organisms hitherto studied.

Notice in the second place the vastly greater complexity of microscopic structure than in any of our former types. The adult organism can no longer be resolved into more or less obvious cells. In the deric, enteric, and cœlomic epithelia we meet with nothing new, but the muscle-plates are not cells, the nephridia show no cell-structure, neither do the nerve-fibres nor the punctate substance of the brain. The body is thus divisible into *tissues* or fabrics each clearly distinguishable from the rest. We have epithelial tissue, cuticular tissue, muscular tissue, and nervous tissue: and the blood and cœlomic fluid are to be looked upon as liquid tissues. One result of this is that, to a far greater extent than in the foregoing types, we can study the morphology of Polygordius under two distinct heads:

anatomy, dealing with the general structure of the parts, and *histology*, dealing with their minute or microscopic structure.

One point of importance must be specially referred to in connection with certain of the tissues It has been pointed out (p. 273) that the epidermis has rather the character of a sheet of protoplasm with regularly-arranged nuclei than of a layer of cells, and that the muscle-plates are covered with a layer of protoplasm with which the ultimate nerve-fibres are continuous (p. 274). Thus certain of the tissues of Polygordius are multinucleate but non-cellular. They are comparable in minute structure to an Opalina or to the plasmodium of a Mycotozoon, and must therefore be distinguished from such definitely cellular tissues as the enteric epithelium.

LESSON XXV

POLYGORDIUS (*Continued*)

ASEXUAL reproduction is unknown in Polygordius, and the organs of sexual reproduction are very simple. The animal is dioecious, gonads of one sex only being found in each individual.

In the species which has been most thoroughly investigated (*P. neapolitanus*) the reproductive products are formed in each metamere from the fourth to the last. Crossing these segments obliquely are narrow bands of muscle (Fig. 70, A, *O.M*) and certain of the cells of cœlomic epithelium covering these bands multiply by fission and form little heaps of cells (*Spy*), each of which is to be looked upon as a gonad. There is thus a pair of gonads to each segment with the exception of the prostomium, the peristomium, the first three metameres, and the anal segment, the reproductive organs exhibiting the same simple metameric arrangement as the digestive, excretory, and circulatory organs. It will be noticed that the primitive sex-cells, arising as they do from cœlomic epithelium, are mesodermal structures, not ectodermal as in hydroids (pp. 231 and 245).

In the male the primitive sex-cells divide and sub-divide, the ultimate products being converted into sperms (Fig. 70,

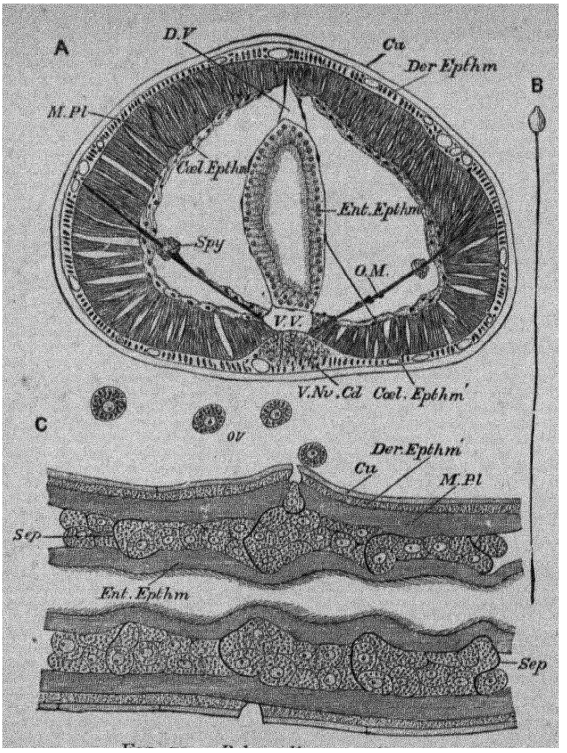

FIG. 70.—*Polygordius neapolitanus.*

A, transverse section of a male specimen to show the position of the immature gonads (*spy*) and the precise form and arrangement of the various layers represented diagrammatically in Fig. 67, C.

The body-wall consists of cuticle (*Cu*), deric epithelium (*Der. Epthm*), muscle-plates (*M. Pl*), and parietal layer of cœlomic epithelium (*Cœl. Epthm*). The ventral nerve cord (*V. Nv. Cd*) is shown to be continuous with the deric epithelium.

The enteric canal consists of ciliated enteric epithelium (*Ent. Epthm*) covered by the visceral layer of cœlomic epithelium (*Cœl. Epthm'*): connecting it with the body-wall are the dorsal and ventral mesenteries formed of a double layer of cœlomic epithelium, and containing respectively the dorsal (*D. V.*) and ventral (*V. V*) blood-vessels.

Passing obliquely across the cœlome are the oblique muscles (*O. M*)

covered with cœlomic epithelium : by differentiation of groups of cells of the latter the spermaries (*Spy*) are formed.

B, a single sperm, showing expanded head and delicate tail.

C, horizontal section of a sexually mature female

The body-wall (*Cu*, *Der. Epthm*, *M. Pl*) has undergone partial histological degeneration, and is ruptured in two places to allow of the escape of the ova (*ov*) which still fill the cœlomic spaces enclosed between the body-wall, the enteric canal (*Ent. Epthm*), and the septa (*Sep*). (After Fraipont.)

B: see p. 255): in the female they enlarge immensely, and take on the character of ova (C, *ov*). Multiplication of the sexual products takes place to such an extent that the whole cœlome becomes crammed full of either sperms or ova (C).

In the female the growth of the eggs takes place at the expense of all other parts of the body, which undergo more or less complete atrophy: the epidermis for instance, becomes liquefied and the muscles lose their contractility. Finally rupture of the body-wall takes place in each segment (C), and through the slits thus formed the eggs escape. So that Polygordius, like an annual plant, produces only a single brood; death is the inevitable result of sexual maturity. Whether or not the same dehiscence of the body-wall takes place in the male is not certain: it has been stated that the sperms make their escape through the nephridia.

Thus while there are no specialized *gonoducts*, or tubes for carrying off the sexual products, it is possible that the nephridia may, in addition to their ordinary function, serve the purpose of male gonoducts or *spermiducts*. Female gonoducts or *oviducts* are however entirely absent.

The ova and sperms being shed into the surrounding water, impregnation takes place, and the resulting oosperm undergoes segmentation or division (see p. 246), a polyplast being formed. The cells of the polyplast become differentiated, an enteron or digestive cavity is formed, and the

embryo is gradually converted into a curious free-swimming creature shown in Fig. 71, A, and called a *trochosphere*.

The trochosphere, or newly-hatched larva of Polygordius (Fig. 71, A) is about $\frac{1}{4}$ mm. in diameter, and has something

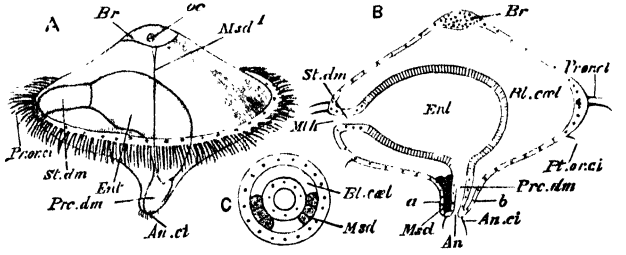

FIG. 71.—A, larva of *Polygordius neapolitanus* in the trochosphere stage; from a living specimen.

B, diagrammatic vertical section of the same: the ectoderm is dotted, the endoderm radially striated, the mesoderm evenly shaded, and the nervous system finely dotted.

C, transverse section through the plane *ab* in B.

The body-wall consists of a single layer of ectoderm cells, which, at the apex of the prostomium (upper hemisphere) are modified to form the brain (*Br*) and a pair of ocelli (*oc*).

The enteric canal consists of three parts: the stomodæum (*St. dm*), opening externally by the mouth (*Mth*), and lined by ectoderm; the enteron (*Ent*) lined by endoderm; and the proctodæum (*Pre. dm*), opening by the anus (*An*) and lined by ectoderm.

Between the body-wall and the enteric canal is the larval body-cavity or blastocœle (*Bl. cœl*).

The mesoderm is confined to two narrow bands of cells (B and C, *Msd*) in the blastocœle, one on either side of the proctodæum; slender mesodermal bands (*Msd'*) are also seen in the prostomium in A.

The cilia consist of a præ-oral circlet (*Pr. or. ci*) above the mouth, a post-oral circlet (*Pt. or. ci*) below the mouth, and an anal circlet (*An. ci*) around the anus.

(A after Fraipont.)

the form of a top, consisting of a dome-like upper portion, the *prostomium*, produced into a projecting horizontal rim; of an intermediate portion or *peristomium*, having the form of an inverted hemisphere; and of a lower somewhat conical

anal region. Around the projecting rim is a double circlet of large cilia (*Pr. or. ci*) by means of which the larva is propelled through the water.

Beneath the edge of the ciliated rim is a rounded aperture, the mouth (*Mth*); this leads by a short, nearly straight gullet (*St. dm*), into a spacious stomach (*Ent*), from the lower side of which proceeds a short slightly curved intestine (*Prc. dm*), opening at the extremity of the conical inferior region by an anus (*An*). Between the body-wall and the enteric canal is a space filled with fluid (*Bl. cœl*), but, as we shall see, this does not correspond with the body-cavity of the adult. The body-wall and the enteric canal consist each of a single layer of epithelial cells, all the tissues included in the adult under the head of mesoderm (p. 275) being absent or so poorly developed that they may be neglected for the present.

Leaving aside all details, it will be seen that the trochosphere of Polygordius is comparable in the general features of its organization to a medusa (compare Fig. 55, p. 241), consisting as it does of an outer layer of cells forming the external covering of the body and of an inner layer lining the digestive cavity. There are, however, two important differences: the space between the two layers is occupied by the mesoglœa in the medusa, while in the worm it is a cavity filled with fluid; and the digestive cavity of the trochosphere has two openings instead of one.

But in order to compare more accurately the medusa with the trochosphere, it is necessary to fill up, by the help of other types, an important gap in our knowledge of the development of Polygordius—the passage from the polyplast to the trochosphere. From what we know of the development of other worms, the process, in its general features, is probably as follows:—

The polyplast is converted, by the accumulation of fluid

in its interior, into a hollow sphere, bounded by a single layer of cells and containing a cavity, the *blastocœle*: this stage of development is called the *blastula*. Next, one side of the blastula becomes tucked in or invaginated so as to convert the embryo from a single-layered sphere into a double-layered cup (Fig. 72, A). This process can be sufficiently well imitated by pushing in one side of a hollow india-rubber ball. The resulting embryonic stage

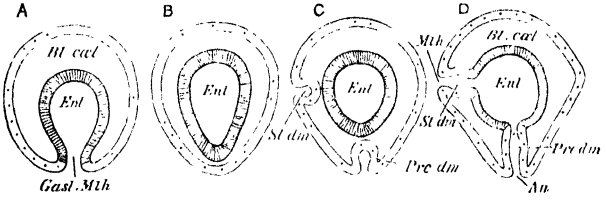

FIG. 72.—Diagram illustrating the origin of the trochosphere from the gastrula. The ectoderm is dotted, the endoderm striated.

A, gastrula, with enteron (*Ent*) and gastrula-mouth (*Gast. Mth*), and with the ectoderm and endoderm separated by the larval body-cavity or blastocœle (*Bl. cœl*).

B, the gastrula-mouth has closed, the enteron (*Ent*) becoming a shut sac.

C, two ectodermal pouches, the stomodæum (*St. dm*) and proctodæum (*Prc. dm*) have appeared.

D, the stomodæum (*St. dm*) and proctodæum (*Prc. dm*) have opened into the enteron (*Ent*), forming a complete enteric canal with mouth (*Mth*) and anus (*An*).

is known as the *gastrula*: its cavity is the enteron (*Ent*) and is bounded by the invaginated cells which now constitute the endoderm, the remaining cells, forming the outer wall of the gastrula, being the ectoderm. The two layers are continuous at the aperture of the cup, the *gastrula-mouth* or *blastopore* (*Gast. Mth*). Between the ectoderm and endoderm is a space, the greatly diminished blastocœle. The resemblance of the gastrula to a simplified Hydra, devoid of tentacles, will be at once apparent

Before long the mouth of the gastrula closes (*B*), the enteron (*Ent*) being thus converted into a shut sac. At about the same time the ectoderm is tucked in or invaginated at two places (*C*), and the two little pouches (*St. dm*, *Prc. dm*) thus formed grow inwards until they meet with the closed enteron and finally open into it (*D*), so that a complete enteric canal is formed—formed, we must not fail to notice, of three distinct parts: (1) an anterior ectodermal pouch, opening externally by the mouth, and distinguished as the *stomodæum*, (2) the enteron, lined with endoderm; and (3) a posterior ectodermal pouch, opening externally by the anus, and called the *proctodæum*.

In the trochosphere (Fig. 71) the gullet is derived from the stomodæum, the stomach from the enteron, and the intestine from the proctodæum; so that only the stomach of the worm-larva corresponds with the digestive cavity of a medusa: the gullet and intestine are structures not represented in the latter form.

Two or three other points in the anatomy of the trochosphere must now be referred to.

At the apex of the dome-shaped prostomium the ectoderm is greatly thickened, forming a rounded patch of cells (Figs. 71 and 73, *Br*), the rudiment of the brain. On the surface of the same region and in close relation with the brain is a pair of small patches of black pigment, the eye-spots or ocelli (*Oc*).

On either side of the intestine, between its epithelium and the external ectoderm, is a row of cells forming a band which partly blocks up the blastocœle (B and C, *Msd*). These two bands are the rudiments of the whole of the mesodermal tissues of the adult—muscle, cœlomic epithelium, &c.—and are hence called mesodermal bands.

Finally on either side of the lower or posterior end of the stomach is a delicate tube (Fig. 73, A, *Nph*) opening by a small aperture on to the exterior, and by a wide funnel-shaped

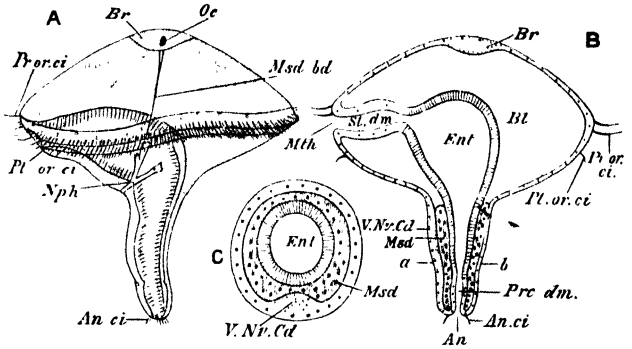

FIG. 73.—A, living specimen of an advanced trochosphere-larva of Polygordius neapolitanus, showing the elongation of the anal region to form the trunk.

B, diagrammatic vertical section of the same : the ectoderm is coarsely, the nervous system finely, dotted, the endoderm radially striated, and the mesoderm evenly shaded.

C, transverse section through the plane *ab* in B.

The pre-oral (*Pr. or. ci*), post-oral (*Pt. or. ci*), and anal (*An. ci*) cilia, brain (*Br*), ocelli (*Oc*), blastocœle (*Bl*), mouth (*Mth*), stomodæum (*St. dm*), proctodæum (*Prc. dm*), and anus (*An*) as in Fig. 71, the enteron (*Ent*) has extended some distance into the trunk.

In A, slender mesodermal bands (*Msd. bd*) in the prostomium, and the branched head-nephridium (*Nph*) are shown.

In B and C the mesoderm (*Msd*) is seen to have obliterated the blastocœle in the trunk-region : the ectoderm has undergone a thickening, forming the ventral nerve-cord (*V. Nv. Cd*).

(A after Fraipont.)

extremity into the blastocœle : it has all the relations of a nephridium, and is distinguished as the *head-nephdridium.*

As the larva of Polygordius is so strikingly different from the adult, it is obvious that development must, in this, as in

several cases which have come under our notice, be accompanied by a metamorphosis.

The first obvious change is the elongation of the conical anal region of the trochosphere into a tail-like portion which may be called the *trunk* (Fig. 73, A). The stomach (enteron), which was formerly confined to the pro- and peri-stomium, has now grown for a considerable distance into the trunk (B, *ent*), so that the proctodæum (*Prc. dm*) occupies only the portion in proximity to the anus.

Important internal changes have also taken place. The deric epithelium or external ectoderm is for the most part composed, as in the preceding stage, of a single layer of cells; but on that aspect of the trunk which lies on the same side as the mouth - *i.e.*, to the left in Fig. 73, A and B—this layer has undergone a notable thickening, being now composed of several layers of cells. This ectodermal thickening is the rudiment of the ventral nerve-cord (*V. Nv. Cd*), and the side of the trunk on which it appears is now definitely marked out as the ventral aspect of the future worm, the opposite aspect—that to the right in the figures—being dorsal. At a later stage two ectodermal cords—the œsophageal connectives—are formed, connecting the anterior end of the ventral nerve-cord with the brain. Note that the two divisions of the central nervous system are originally quite distinct.

The mesodermal bands, which were small and quite separate in the preceding stage (Fig. 71, B and C, *Msd*). have now increased to such an extent as completely to surround the enteron and obliterate the blastocœle (Fig. 73, B and C, *Msd*). At this stage therefore there is no body-cavity in the trunk, but the space between the deric and enteric epithelia is occupied by a solid mass of mesoderm.

In a word, the larva is at present, as far as the trunk is concerned, triploblastic but *acœlomate*.

Development continues, and the larva assumes the form shown in Fig. 74, A. The trunk has undergone a great increase in length and at the same time has become divided by a series of annular grooves into segments or metameres, like those of the adult worm but more distinct (compare Fig. 66, D, p. 269). By following the growth of the larva from the preceding to the present stage, it is seen that these segments are formed from before backwards, *i.e.*, the segment next the peristomium is the oldest, and new ones are continually being added between the last formed and the extremity of the trunk, or what may now be called the anal segment. By this process the larva has assumed the appearance of a worm with an immense head and a very slender trunk.

The original larval stomach (enteron) has extended, with the formation of the metameres, so as to form the greater portion of the intestine: the proctodæum (*Prc. dm*) is confined to the anal segment.

Two other obvious changes are the appearance of a pair of small slender processes (A, *t*)—the rudiments of the tentacles—on the apex of the prostomium, and of a circlet of cilia (*Pr. an. ci*) round the posterior end of the trunk.

The internal changes undergone during the assumption of the present form are very striking. In every fully formed metamere the mesoderm—solid, it will be remembered, in the previous stage—has become divided into two layers, a somatic layer (B and C, *Msd* (*som*)) in contact with the ectoderm and a splanchnic layer (*Msd* (*spl*)) in contact with the endoderm. The space between the two layers (*Cœl*) is the permanent body-cavity or cœlome, which is

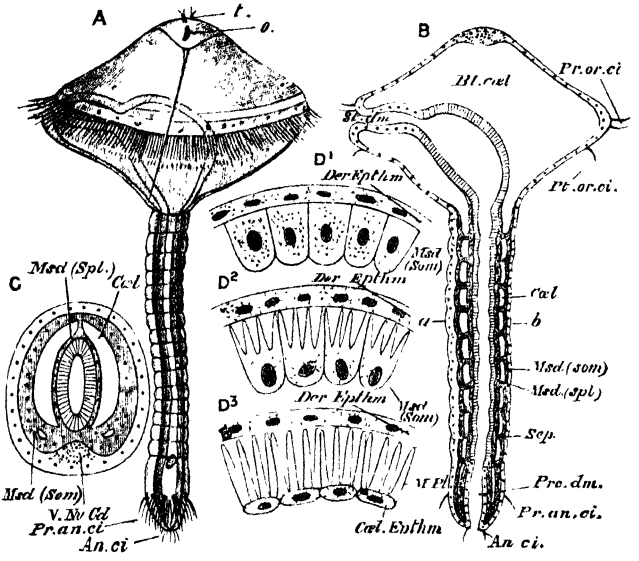

FIG. 74.—A, larva of Polygordius neapolitanus in a condition intermediate between the trochosphere and the adult worm, the trunk-region being elongated and divided into metameres.

B, diagrammatic vertical section of the same: the ectoderm is coarsely, the nervous system finely, dotted, the endoderm radially striated, and the mesoderm evenly shaded.

C, transverse section along the plane *ab* in B.

The pre-oral (*Pr. or. ci*), post-oral (*Pt. or. ci*), and anal (*An. ci*) cilia, the blastocœle (*Bl. cœl*), stomodæum (*St. dm*), and proctodæum (*Prc. dm*) are as in Fig. 71, A and B: the enteron now extends throughout the segmented region of the trunk.

A pair of tentacles (*t*) has appeared on the prostomium near the ocelli (*o*), and a pre-anal circlet of cilia (*Pr. an. ci*) is developed.

The mesoderm has divided into somatic (*Msd* (*som*)) and splanchnic (*Msd* (*spl*)) layers with the cœlome (*Cœl*) between: the septa (*Sep*) are formed by undivided plates of mesoderm separating the segments of the cœlome from one another.

D¹–D³, three stages in the development of the somatic mesoderm. In D¹ it (*Msd* (*Som*)) consists of a single layer of cells in contact with the deric epithelium (*Der. Epthm*): in D² the cells have begun to split up in a radial direction: in D³ each has divided into a number of radially arranged sections of muscle-plates (*M. Pl*) and a single cell of cœlomic epithelium (*Cœl. Epthm*).

(A after Fraipont.)

thus quite a different thing from the larval body-cavity or blastocœle, being formed, not as a space between ectoderm and endoderm, but by the splitting of an originally solid mesoderm.

The division of the mesoderm does not however extend quite to the middle dorsal and middle ventral lines: in both these situations a layer of undivided mesoderm is left (c), and in this way the dorsal and ventral mesenteries are formed. Spaces in these, apparently the remains of the blastocœle, form the dorsal and ventral blood-vessels. Moreover the splitting process takes place independently in each segment, and a transverse vertical layer of undivided mesoderm (B, *Sep*) is left separating each segment from the adjacent ones before and behind: in this way the septa arise.

The nephridia appear to have a double origin, the superficial portion of each being formed from ectoderm, the deep portion, including the nephrostome, from the somatic layer of mesoderm.

In the ventral nerve-cord the cells lying nearest the outer surface have enlarged and formed nerve-cells, while those on the dorsal aspect of the cord have elongated longitudinally and become converted into nerve-fibres. This process has already begun in the preceding stage.

But the most striking histological changes are those which gradually take place in the somatic layer of mesoderm. At first this layer consists of ordinary nucleated cells (D^1, *Msd Som*), but before long each cell splits up in a radial direction (D^2) from without inwards -*i.e.*, from the ectoderm (*Der. Epthm*) towards the cœlome—finally taking on the form of a book with four or more slightly separated leaves directed outwards or towards the surface of the body, and with its back—the undivided portion of the cell—bounding

the cœlome. The cells being arranged in longitudinal series, we have a number of such books placed end to end in a row with the corresponding leaves in contact—page one of the first book being followed by page one of the second, third, fourth, &c., page two by page two, and so on through one or more segments of the trunk. Next, what we have compared with the leaves of the books—the divided portions of the cells—become separated from the backs—the undivided portions (D^3)—and each leaf (*M. Pl*) fuses with the corresponding leaves of a certain number of books in the same longitudinal series. The final result is that the undivided portions of the cells (backs of the books, *Cœl. Epthm*) become the parietal layer of cœlomic epithelium, the longitudinal bands formed by the union of the leaves (*M. Pl*) becoming the muscle-plates, which are thus *cell-fusions*, each being formed by the union of portions of a series of longitudinally arranged cells.

At the same time the cells of the splanchnic layer of mesoderm thin out and become the visceral layer of cœlomic epithelium

We see then that by the time the larva has reached the stage shown in Fig. 74, it is no longer a mere aggregate of simple cells arranged in certain layers. The cells themselves have undergone differentiation, some becoming modified into nerve-fibres, others by division and subsequent fusion with their neighbours forming muscle-plates, while others, such as the epithelial cells, remain almost unaltered.

Thus, in the course of the development of Polygordius, cell-multiplication and cell-differentiation go hand in hand, the result being the formation of those complex tissues the presence of which forms so striking a difference between the worm and the simpler types previously studied.

It is important to notice that this comparatively complex animal is in one stage of its existence—the oosperm—as simple as an Amœba; in another—the polyplast—it is comparable to a Pandorina, and in a third—the blastula—to a Volvox; in a fourth—the gastrula—it corresponds in general features with a Hydra; while in a fifth—the trochosphere—it resembles in many respects a Medusa. As in other cases we have met with, the comparatively highly-organised form passes through stages in the course of its individual development similar in general characters to those which, on the theory of evolution, its ancestors may be considered to have passed through in their gradual ascent from a lower to a higher stage of organization.

The rest of the development of Polygordius may be summarized very briefly. The trunk grows so much faster than the head (pro-*plus* peri-stomium)—that the latter undergoes a relative diminution in size, finally becoming of equal diameter with the trunk, as in the adult. The ciliated rings are lost, the tentacles grow to their full size, the eye-spots atrophy, and thus the adult form is assumed.

LESSON XXVI

THE CHIEF DIVISIONS OF THE ANIMAL KINGDOM: THE STARFISH

THE student who has once thoroughly grasped the facts of structure of such typical unicellular animals as Amœba and the Infusoria, of such typical diploblastic animals as Hydra and Bougainvillea, and of such a typical triploblastic animal as Polygordius, ought to have no difficulty in understanding the general features of the organization of any other members of the animal kingdom. When once the notions of a cell, a cell-layer, a tissue, an organ, body-wall, enteron, stomodæum, proctodæum, cœlome, somatic and splanchnic mesoderm, are fairly understood, all other points of structure become hardly more than matters of detail.

If we turn to a text-book of Zoology we shall find that the animal kingdom is roughly divisible into eight primary sub-divisions, called sub-kingdoms, types, or phyla. These are as follows:—

Protozoa.
Porifera.
Cœlenterata.
"*Vermes.*"
Echinodermata.
Arthropoda.
Mollusca.
Vertebrata.

With a few exceptions, the discussion of which would be out of place here, the vast number of animals known to us may be arranged in one or other of these groups.

The *Protozoa* are animals which are either unicellular in the strict sense, or non-cellular, or colonies of unicellular zooids: they have been represented in previous lessons by Amœba and Protamœba, Hæmatococcus, Heteromita, Euglena, the Mycetozoa, Paramœcium, Stylonychia, Oxytricha, Opalina, Vorticella, Zoothamnium, the Foraminifera, the Radiolaria, Pandorina, and Volvox. The reader will therefore have no difficulty in grasping the general features of this phylum.

The *Cœlenterata* are the diploblastic animals, and have also been well represented in the foregoing pages, namely by Hydra, Bougainvillea, Diphyes, and Porpita. The sea-anemones and corals also belong to this phylum, in which also the *Porifera* or sponges were formerly included.

The "*Vermes*," or Worms, are a very heterogeneous assemblage. They are all triploblastic, but while some are cœlomate, others have no body-cavity; some, again, are segmented, others not. Still, if the structure of Polygordius is thoroughly understood, there will be little difficulty in understanding that of a fluke, a tape-worm, a round-worm, an earthworm, or one of the ordinary marine worms.

Of the remaining four sub-kingdoms we have, so far, studied no example, but a brief description of a single example of each will show how they all conform to the general plan of organisation of Polygordius, being all triploblastic and cœlomate.

Under the *Echinodermata* are included the various kinds of starfishes—sand-stars, brittle-stars, and feather-stars, as well as sea-urchins, sea-cucumbers, &c. A starfish will serve as an example of the group.

The phylum *Arthropoda* includes crayfishes, lobsters, crabs, shrimps, prawns, wood-lice, and water-fleas; scorpions, spiders, and mites; centipedes and millipedes; and all kinds of insects, such as cockroaches, beetles, flies, ants, bees, butterflies, and moths. A crayfish forms a very fair example of the aquatic kinds (*Crustacea*).

In the phylum *Mollusca* are included the ordinary bivalves, such as mussels and oysters; snails, slugs, and other univalves or one-shelled forms; and cuttle-fishes, squids, and Octopi. An account of a fresh water mussel will serve to give a general notion of the character of this group.

Finally, under the head of *Vertebrata* are included all the backboned animals: the lampreys and hags; true fishes, such as the shark, skate, sturgeon, cod, perch, trout, &c.; amphibians, such as frogs, toads, newts, and salamanders; true reptiles, such as lizards, crocodiles, snakes, and tortoises; birds; and mammals, or creatures with a hairy skin which suckle their young, such as the ordinary hairy quadrupeds, whales and porpoises, apes, and man. The essential structure of a vertebrate animal will be understood from a brief description of a dog fish.

The Starfish.

The commonest British starfish is *Asterias rubens*, but the main features of the following description will apply to any species. The starfish consists of a central disc-like portion, from which radiate five arms or rays. The animal crawls over the rocks with its flat, light-coloured ventral surface downwards, and with its darker, convex, dorsal surface upwards. It can move in any direction, so that, in the ordinary sense of the words, anterior and posterior extremities cannot be distinguished. Radial symmetry such

as this, *i.e.*, the division of the body into similar parts radiating from a common centre, is characteristic of the Echinodermata generally.

In the centre of the disc on the ventral surface is a five-sided depression, at the bottom of which is the large mouth (Fig. 75 and Fig. 76, A, *Mth*). From it radiate five grooves

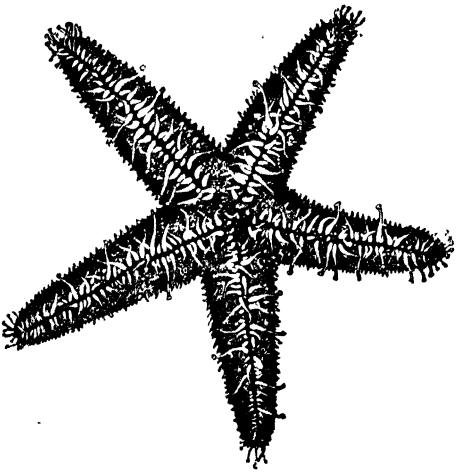

FIG. 75.—A Starfish, from the ventral aspect, showing the disc and arms, the central mouth, and the numerous tube-feet. (From Parker and Haswell's *Zoology*, after Leuckart and Nitsche.)

called the *ambulacral grooves*, one along the ventral surface of each arm (Fig. 76, A and B). In the living animal numerous delicate semi-transparent cylinders, the *tube-feet* (Fig. 75 and Fig. 76, *T. F*), are protruded from these grooves; they are very extensible and each ends in a sucker It is by moving these structures in various directions, protruding some and withdrawing others, that the starfish is able to move along

either a horizontal or a vertical surface, and even to turn itself over when placed with the ventral side upwards.

Near the middle of the disc, on the dorsal surface, is the very minute anus (Fig. 76 A, *An*) ; it is situated on a line drawn from the centre of the disc to the re-entering angle between two of the rays, and is therefore said to be inter-radial in position. Near the anus, and also inter-radially situated, is a circular calcareous plate, the *madreporite* (*Mdpr*), perforated by numerous microscopic apertures. The presence of this structure disturbs the radial symmetry of the starfish and gives rise to a bilateral symmetry, since the animal can be divided into two truly equal halves by a single plane only, *viz.*, the plane passing through the middle of the madreporite and of the arm opposite to it.

The body, though flexible, is tolerably firm and resistant, owing to the fact that immediately beneath the soft, slimy skin there is a layer of little irregular calcareous bodies, the *ossicles* (Fig. 76, *os*), forming a kind of scale armour. Many of them give attachment to spines, and between them are minute apertures, the *dermal pores*, through which, during the life of the animal, are protruded delicate, glove-finger-like processes, the *dermal gills* or *respiratory cæca* (*Resp. cæ*). Both on the dorsal and the ventral surfaces are found curious and characteristic organs called *pedicellariæ* (*Ped*). These are minute forceps-like structures, consisting of a basal piece or stalk and of two jaws, each supported by a calcareous plate: the jaws are worked by muscles, and apparently serve to remove fæcal matter, foreign bodies, &c., from the surface of the animal.

The tube-feet, already referred to, are arranged symmetrically on either side of each ambulacral groove. At the extremity of the groove is a single structure (*t*) like a tube-foot without the terminal sucker: it is called the *tentacle*,

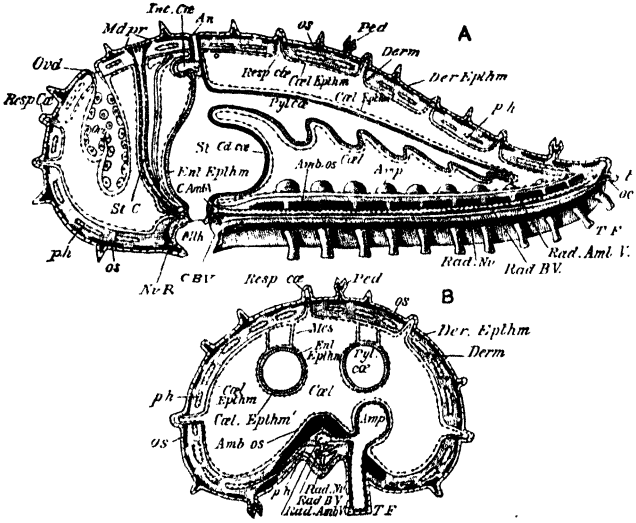

FIG. 76.—Diagrammatic sections of a Starfish.

A, vertical section passing on the right through a radius, on the left through an inter-radius. The off-side of the ambulacral groove, with the tube feet (*T. F*) and ampullæ (*Amp*), is shown in perspective.

B, transverse section through an arm.

The ectoderm is coarsely dotted, the nervous system finely dotted, the endoderm radially striated, the mesoderm evenly shaded, the ossicles of the skeleton black, and the cœlomic epithelium represented by a beaded line.

The body-wall consists of deric epithelium (*Der. Epthm*), dermis (*Derm*), and the parietal layer of cœlomic epithelium (*Cœl. Epthm*).

To the body-wall are attached pedicellariæ (*Ped*), and the end of the arm bears a tentacle (*t*) with an ocellus (*oc*) at its base.

The skeleton consists of ossicles (*os*) imbedded in the dermis: large ambulacral ossicles (*Amb. os*) bound the ambulacral grooves on the ventral surfaces of the arms.

The mouth (*Mth*) leads by a short gullet into a stomach (*St*), which gives off a cardiac cæcum (*Cd. cæ*) and a pair of pyloric cæca (*Pyl. cæ*) to each arm, and passes into an intestine (*Int*) which gives off intestinal cæca (*Int. cæ*) to the inter-radii, and ends in the anus (*An*). The pyloric cæca are connected to the dorsal body-wall by mesenteries (*Mes.* in B). The wall of the enteric canal consists of enteric epithelium covered by the visceral layer of cœlomic epithelium (*Cœl. Epthm'*).

From the cœlome are given off respiratory cæca (*Resp. cæ*), which project through the body-wall: the latter contains spaces (*p. h*) derived from the cœlome.

The circular blood-vessel (*C. B. V*) surrounds the gullet and gives off radial vessels (*Rad. B. V*) to the arms and an inter-radial plexus connected with a pentagonal ring round the intestine.

The circular ambulacral vessel (*C. Amb. V*) gives off radial vessels (*Rad. Amb. V*) to the arms connected with the ampullæ (*Amp*) and tube-feet (*T. F*): it is also connected with the stone-canal (*St. C*), which opens externally by the madreporite (*Mdpr*).

The nerve ring (*Nv. R*) gives off radial nerves (*Rad. Nv*) to the arms.

The ovary (*Ovy*) is inter-radial, and opens by a dorsal oviduct (*Ovd*).

and is probably an organ of smell. At the base of the tentacle is a bright red eye-spot (*oc*).

Sections show that there is a well-marked cœlome, separating the body-wall from the enteric canal and containing the gonads, blood-vessels, &c. The body-wall consists externally of a very thin cuticle, then of a layer of deric epithelium or epidermis (*Der. Epthm*), then of a thick, double, fibrous layer (*Derm*), then of a thin and interrupted layer of muscle, and finally, of a layer of cœlomic epithelium (*Cœl. Epthm*) bounding the body-cavity.

The ossicles with their spines together form an external skeleton or *exoskeleton*: as already mentioned they are, for the most part, small irregular bodies developed in the fibrous layer of the body-wall, and overlapping one another in a scale-like fashion. But the ambulacral grooves are bounded by regularly arranged pairs of large, rod-like *ambulacral ossicles* (*Amb. os*), arranged like rafters, the dorsal ends of each pair uniting at the summit of the groove, while their ventral ends diverge and are connected with the ordinary ossicles at the edge of the arm. Between each ambulacral ossicle and its predecessor and successor in the row is an aperture, the *ambulacral pore*, with which one of the tube-feet is connected.

The mouth (Fig. 76, A, *mth*) leads by a short gullet into a stomach (*st*) divisible into two portions, called respectively

the *cardiac* and *pyloric* divisions. The cardiac division (Fig. 77, *card. st*), into which the gullet opens, is a spacious sac, produced into five wide pouches, the *cardiac cæca* (Fig. 76, A, *Cd. cæ*; Fig. 77), one of which extends into the

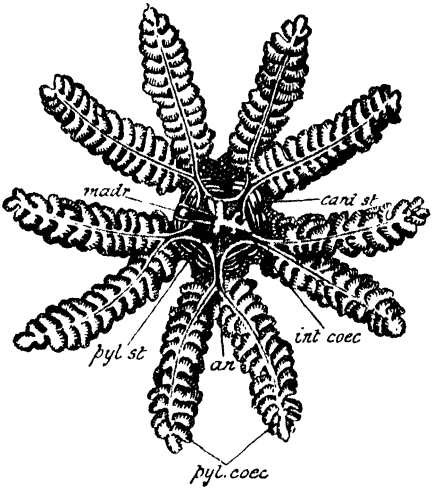

FIG. 77.—Digestive organs of a Starfish (*Asterias rubens*), seen from the dorsal aspect.

The cardiac portion of the stomach (*card. st*) gives off five short cardiac cæca or pouches and leads into the pyloric division (*pyl. st*), from which five bifid pyloric cæca (*pyl. cæc*) are continued to the ends of the arms. The short intestine is recognisable by the presence of the intestinal cæca (*int. cæc*) and of the anus (*an*): *madr*, madreporite. (From Parker and Haswell's *Zoology*, after Leuckart.)

base of each arm. When the starfish is feeding it can evert this cardiac sac over the shellfish or other object serving as prey, and is thus able to devour animals too large to be taken into the mouth: the everted stomach is afterwards drawn back by means of special muscles. Dorsally the

cardiac communicates with the small pyloric division (Fig. 77, *pyl. st*), which also gives off five pouches, the *pyloric cæca* (Fig. 76 and 77, *pyl. cæ*); but each of these, instead of extending merely into the base of the corresponding arm, divides into two, and both branches extend to the extremity of the arm, giving off as they go small side-branches, so that the whole cæcum has a tufted or sacculated character. The pyloric cæca are lined by gland-cells, and in them the digestion of the food takes place. They are connected with the dorsal walls of the arms by mesenteries (Fig. 76, B, *mes*).

The pyloric division of the stomach leads into a very short *intestine* which passes upwards in a straight line to the anus (*an*), previously giving off two intestinal cæca (*int. cæ*) situated inter-radially—not radially like the blind offshoots of both divisions of the stomach.

The whole enteric canal is lined with enteric epithelium (Fig. 76, *Ent. Epthm*), and is covered by the visceral layer of cælomic epithelium (*Cœl. Epthm'*): it has no muscular layer. There is a spacious cœlome (*Cœl*) between the body-wall and the enteric canal filled with a watery fluid containing leucocytes. The cœlomic epithelium is ciliated, the cilia effecting a circulation of the cœlomic fluid. The dermal gills (*Resp. cæ*), already referred to, communicate with the cœlome, and are, in fact, hollow outpushings of the body-wall. They serve to bring the cœlomic fluid into close relation with the surrounding water, and are therefore to be looked upon as *organs of respiration*.

One of the most characteristic structures in the anatomy of the starfish is a peculiar system of vessels called the *water-vascular* or *ambulacral system*: it is of great functional importance, being connected with the working of the tube-feet.

The central part of the ambulacral system is a pentagonal tube (Fig. 78, *c;* Fig. 76, *C. Amb. V*) which surrounds the gullet, and is called the *ambulacral ring-vessel.* From each angle of the pentagon is given off a *radial ambulacral vessel*

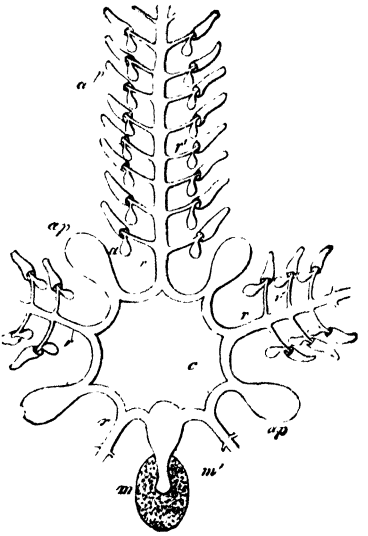

FIG. 78.—The water vascular system of a Starfish (diagramatic).
The ring-vessel (*c*) gives off five radial vessels (*r*), lateral off-shoots of which (*r'*) are connected with the tube-feet (*p*) and ampullæ (*a*).
Inter-radially the ring-vessels give off Polian vesicles (*ap*) and the madreporic canal (*m'*) ending in the madreporite (*m*). (From Gegenbaur.)

(Fig. 78, *r;* Fig. 76, *Rad. Amb. V*) which proceeds to the end of the corresponding arm, lying in the dihedral angle included by the double row of ambulacral ossicles, and consequently external to this portion of the skeleton (Fig. 76, B). Each radial vessel sends off side branches (Fig. 78, *r'*)

which communicate with the hollow tube-feet (Fig. 78, *p*; Fig. 76, *T. F.*), and each tube-foot is connected by a narrow canal passing through an ambulacral pore (p. 310) with a bladder-like body, the *ampulla* (Fig. 78, *a*; Fig. 76, *Amp*) lying in the cœlome. The ampullæ consequently form a double row of bladders along the ventral region of the interior of the arm.

The ring-vessel also gives off inter-radially, *i.e.*, in the intervals between the arms, bladder-like bodies, the *Polian vesicles* (Fig. 78, *ap*), one or two in each inter-radius. In one of the inter-radii there also goes off from the ring-vessel a tube, called the *stone-canal* (Fig. 78, *m'*; Fig. 76, *St. c*) from the fact that its walls are calcified, which passes directly upwards and becomes connected with the madreporite (Fig. 78, *m*; Fig. 76, A, *Mdpr*). The latter is perforated by minute apertures which are in communication with the cavity of the stone-canal, and in this way the ambulacral system is placed in direct communication with the surrounding water.

The whole ambulacral system contains a watery fluid, and its walls consist of a lining of epithelium and an outer muscular layer particularly well developed in the ampullæ and tube-feet. Contraction of the muscles of the ampullæ forces water into the tube-feet, and causes protrusion of these organs: their withdrawal is brought about by the contraction of the longitudinal muscles in their walls, by which the fluid is forced back into the ampullæ.

Thus the whole ambulacral system forms an elaborate locomotory apparatus worked by water-power. It is quite confined to Echinoderms. In all the other higher animals movements are effected by the direct, and not, as in this case, by the indirect action of muscles.

A second system of vessels constitutes the so-called *blood-system*. Surrounding the gullet below the ambulacral

ring-vessel is a *ring blood-vessel* (Fig. 76, A, *C. B. V*), sending off *radial blood-vessels* (*Rad. B. V*) to the arms. An *inter-radial sinus* or blood-space lies alongside the stone canal, surrounding the ovoid gland (see p. 316), and is connected below with the ring-vessel and above with a pentagonal vessel or sinus, from which inter-radial branches proceed to the gonads.

The *nervous system* is considerably simpler than that of Polygordius. It consists, in the first place, of a pentagonal *nerve-ring* (Fig. 76, A, *Nv. R*) surrounding the mouth, and having the character of a mere thickening of the deric epithelium. From each of its angles goes off a *radial nerve* (*Rad. Nv*) which passes along the arm below the ambulacral and blood-vessels, and is also nothing more than a thickening of the epidermis, some of the cells of which are modified into nerve-cells and fibres. At the end of the arm the radial nerve terminates in the eye-spot. In addition to this superficial nervous system there is a deep nervous system, situated internally to the former, and consisting of a double pentagon round the mouth, sending off double radial nerves to the arms. There are also scattered nervous elements in the dorsal region of the body-wall.

Like Polygordius, the starfish is diœcious: there is no external distinction between the sexes, and even the ovaries and spermaries can be distinguished only by microscopical examination. There are five pairs of gonads ovaries (Fig. 76, A, *ovy*) or spermaries as the case may be one pair in each inter-radius. Each gonad has the form of a bunch of grapes, being a much-lobed sac lined by epithelium from which the ova or sperms are developed. It is continued into a tube or *gonoduct*, called *spermiduct* in the male, *oviduct* (*Ovd*) in the female, which opens inter-radially on the dorsal surface close to the bases of the arms. The

gonads are all connected by cords of tissue with an organ called the *axial organ*, which lies alongside the stone-canal and is surrounded by a blood-sinus. Its function is not known with certainty.

The ova and sperms are shed into the water, where im-

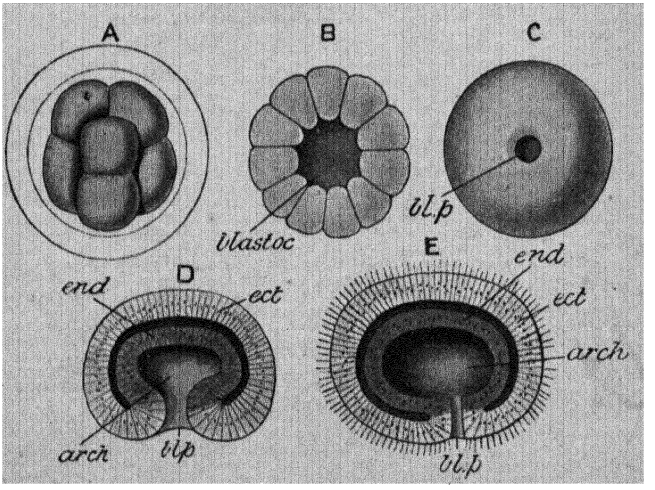

FIG. 70. —Early stages in the development of a Starfish.

A. The polyplast, surrounded by the vitelline membrane.

B. The blastula, in section.

C. The gastrula, external view, showing the blastopore (*bl. p*).

D. The gastrula, in vertical section; *arch*, enteron.

E. More advanced gastrula, with ciliated ectoderm.

Arch, enteron; *blastoc*, blastocœle; *bl.p.* blastopore; *ect*, ectoderm; *end*, endoderm.

(From Parker and Haswell's *Zoology*.)

pregnation takes place. The oosperm undergoes the usual process of segmentation, forming a polyplast (Fig. 79, A), which is soon converted into a blastula (B) by the cells arranging themselves round a central cavity. One side of the blastula becomes invaginated or tucked in, and a gastrula

(C, D, E) is formed, the cells becoming differentiated into ectoderm and endoderm, and the ectoderm cells acquiring cilia. The gastrula gradually takes on the form of a peculiar free-swimming larva having a certain general resemblance to the trochosphere and called a *bipinnaria* (Fig. 80): it differs from the adult starfish in showing no trace of radial symmetry, the body being produced into several ciliated

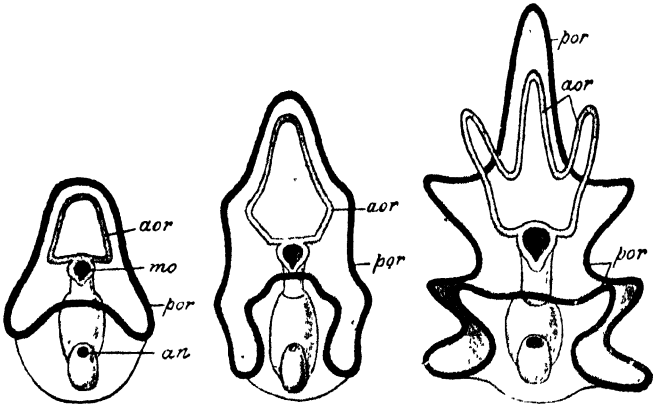

FIG. 80.—Three stages in the development of the Bipinnaria larva of a Starfish. *An*, anus; *aor*, pre-oral ciliated ring; *mo*, mouth; *por*, post-oral ciliated ring. (From Parker and Haswell, after Leuckart and Nitsche.)

processes or arms, all bilaterally arranged, and the enteric canal having the form of a curved cylindrical tube, consisting of gullet, stomach, and intestine lying in the median plane. The bipinnaria lives a free life for a time, swimming by means of its cilia, and finally, by a complex series of changes, undergoes gradual metamorphosis into the adult starfish.

LESSON XXVII

THE CRAYFISH

THE Starfish has furnished us with an example of an animal in which an obvious radial symmetry is, as it were, superposed upon an original bilateral symmetry: in which also there is an extremely simple form of nervous system, a unique type of locomotory apparatus, and no trace of metameric segmentation. We have now to study, in the crayfish, an animal formed upon quite the same general plan of structure as Polygordius as to segmentation, arrangement of organs, &c., but which reaches, in every respect, a far higher grade of organisation.

The Common British Fresh-water Crayfish is *Astacus fluviatilis*: allied species occur in Europe, Asia, and America. The following description will apply almost equally well to the Lobster, *Homarus vulgaris*.

The body of the crayfish (Fig. 81) is divided into two regions, an anterior, the *cephalothorax*, which is unjointed and is covered by a cuirass-like structure, the *carapace*, and a posterior, the *abdomen*, which is divided into distinct segments, movable upon one another in a vertical plane. The cephalothorax is again divided into two regions, an anterior, the *head* (*cth*), and a posterior, the *thorax* (*kd*), by a trans-

verse depression, the *cervical groove*. The carapace is developed from the dorsal and lateral regions of both head and thorax: it is free at the sides of the thorax, where it

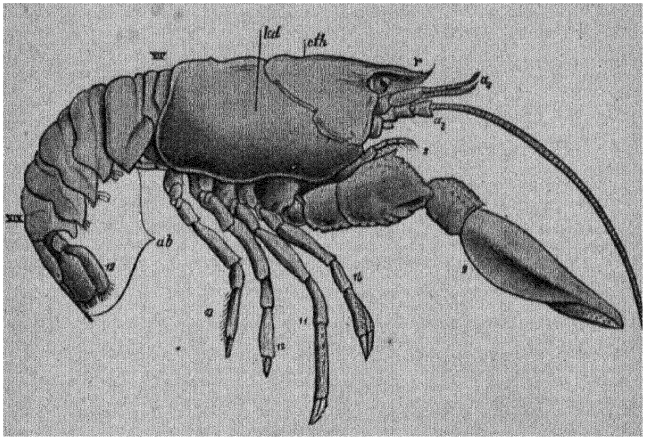

FIG. 81.—Side view of male Freshwater Crayfish, natural size.

The cephalothorax is covered by the carapace, produced in front into a rostrum (*r*) and divisible into cephalic (*cth*) and thoracic (*thd*) portions separated by an oblique cervical groove. The line from *hd* points to the gill-cover.

The abdomen (*ab*) is made up of six movably articulated segments (xiv–xix), followed by a telson, the extremity of which is indicated by the lower end of the bracket from *ab*.

The eye-stalk is seen at the base of the rostrum.

Of the cephalic appendages the antennule (a^1) and antenna (a^2) are shown; of the thoracic appendages the third maxilliped (8), the enlarged first leg or cheliped (9), and the four slender walking legs (10–13); of the abdominal appendages three pleopods and the uropod (18).

(From Lang, after Huxley.)

forms a flap or *gill-cover* (Fig. 83, B, *Br.cg*) on each side, separated from the actual body wall by a narrow space in which the gills are contained

or *appendages*, structures which we have not hitherto met with. Both trunk and appendages are covered with a sort of shell, formed of a substance called *chitin*, strongly impregnated with carbonate of lime so as to be hard and but slightly elastic.

The abdomen is made up of seven segments: the first six of these (Fig. 81, xiv–xix) are to be considered as metameres in the sense in which the word is used in the case of Polygordius. Each has a ring-like form, presenting a broad dorsal region or *tergum*; a narrow ventral region or *sternum*, and downwardly directed lateral processes, the *pleura*. The seventh division of the abdomen is the *telson*: it is flattened horizontally and divided by a transverse groove into anterior and posterior portions. All seven segments are calcified, and are united to one another by chitinous articular membranes: the first segment is similarly joined to the thorax. Thus the exoskeleton of the Crayfish is a continuous structure, but is discontinuously calcified so as to have the character of a hard jointed armour.

It has been stated that the abdominal segments are movable upon one another in a vertical plane, *i.e.*, the whole abdomen can be *extended* or straightened, and *flexed* or bent under the cephalothorax: the segments are incapable of movement from side to side. This is due to the fact that, while adjacent segments are connected dorsally and ventrally by flexible articular membranes, they present at each side a *joint*, placed at the junction of the tergum and pleuron, and formed by a little peg-like process of one segment fitting into a depression or socket in the other. A line drawn between the right and left joints constitutes the *axis of articulation*, and the only possible movement is in a plane at right angles to this axis.

Owing to the presence of the carapace the *thoracic region*

is immovable, and shows no distinction into segments either on its dorsal (tergal) or lateral (pleural) aspect. But on the ventral surface the sterna of the thoracic segments are clearly marked off by transverse grooves, and the hindmost of them is slightly movable Altogether eight thoracic segments can be counted.

The ventral and lateral regions of the thoracic exoskeleton are produced into the interior of the body in the form of a segmental series of calcified plates, so arranged as to form a row of lateral chambers in which the muscles of the limbs lie, and a median tunnel-like passage or *sternal canal*, containing the thoracic portion of the nervous system. The entire *endophragmal system*, as it is called, constitutes a kind of internal skeleton (Fig. 83, B).

The *head* exhibits no segmentation: its sternal region is formed largely by a shield-shaped plate, the *epistoma*, nearly vertical in position. The ventral surface of the head is, in fact, bent so as to face forwards instead of downwards. The cephalic region of the carapace is produced in front into a large median spine, the *rostrum* (Fig. 81, *r*): immediately below it is a plate from which spring two movably articulated cylindrical bodies, the *eye-stalks*, bearing the eyes at their ends.

The appendages have very various forms, and are all, like the abdomen, jointed or segmented, being divisible into freely articulated limb-segments or *podomeres*. The observer is at once struck by the long feelers attached to the head, the five pairs of legs springing from the thorax, and the little fin-like bodies arising from the sterna of the abdomen. It will be convenient to begin with the last-named region.

The third, fourth, and fifth segments of the abdomen bear each a pair of small appendages, the swimming-feet or *pleopods*. A pleopod (Fig. 82, 10) consists of an axis or

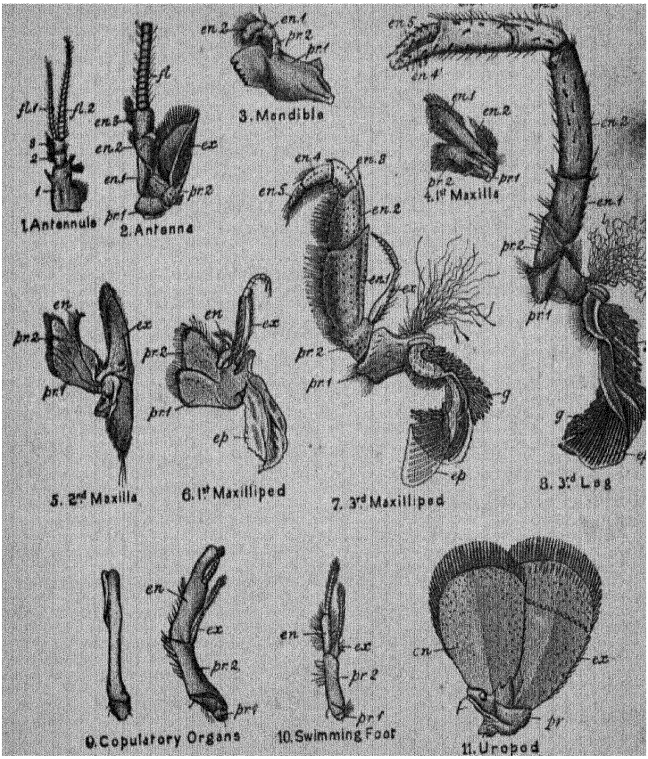

FIG. 82.—The principal appendages of the fresh-water Crayfish placed in the same position, with the protopodite (*pr*) and epipodite (*ep*) downwards, the endopodite (*en*) to the left, and the exopodite (*ex*) to the right.

The protopodite is typically formed of two podomeres (*pr.* 1, *pr.* 2), the endopodite of five (*en.* 1–*en.* 5): a gill (*g*) may be attached to the epipodite and a bunch of long setæ to the protopodite (7 and 8).

The three segments of the antennule are marked 1–3, its flagella *fl.* 1 and *fl.* 2: at the distal end of the endopodite of the antenna is a flagellum (*fl*).

(From Parker and Haswell's *Zoology*, after Huxley.)

protopodite having a very short proximal (*pr.* 1), and a long distal (*pr.* 2) podomere, and bearing at its free end two jointed plates, fringed with setæ, the *endopodite* (*en*) and *exopodite* (*ex*). These appendages act as fins, moving backwards and forwards with a regular swing, and probably aiding in the animal's forward movements.

In the female a similar appendage is borne on the second segment, while that of the first is more or less rudimentary. In the male the first and second pleopods (9) are modified into incomplete tubes which act as copulatory organs, serving to transfer the spermatophores to the body of the female. The sixth pair of pleopods (11) are alike in the two sexes: they are very large, both endo- and exopodite having the form of broad flat plates: in the natural position of the parts they lie one on each side of the telson, forming with it a large five-lobed tail fin: they are therefore conveniently called *uropods* or tail-feet. The telson itself bears no appendages.

The thoracic appendages are very different. The four posterior segments bear long slender, jointed *legs* (Fig. 81, 8), upon which the animal walks: in front of these is a pair of very large legs terminating in huge claws or *chelæ*, and hence called *chelipeds*. The three anterior segments bear much smaller appendages (6, 7) more or less leg-like in form, but having their bases toothed to serve as jaws: they are distinguished as *maxillipeds* or foot-jaws.

The structure of these appendages is best understood by a consideration of the *third maxilliped* (Fig. 82, 7). The main portion of the limb is formed of seven podomeres arranged in a single series, strongly calcified, and, with the exception of the second and third, which are fused, movably articulated with one another. The second podomere, counting from the proximal end, bears a many-jointed

feeler-like organ (*ex*), and from the first springs a thin, folded plate (*ep*) having a plume-like gill (*g*) attached to it. The first two segments of the axis form the protopodite, its remaining five segments the endopodite, and the feeler, which is directed outwards, or away from the median plane, the exopodite. The folded plate is called the *epipodite:* in the natural position of the parts it is directed upwards, and lies in the gill-cavity between the proper wall of the thorax and the gill-cover (Fig. 87, A, *pbd.*).

The five *legs* (8) differ from the third maxilliped in their greater size, and in having no exopodite: in the fifth or last the epipodite also is absent. The first three of them have undergone a curious modification, by which their ends are converted into pincers or *chelæ:* the fourth segment of the endopodite (sixth of the entire limb, *en.* 4) is produced distally so as to form a claw-like projection (*en.* 4′), against which the terminal segment (*en.* 5) bites. The first leg is much stouter than any of the others, and its chela is of immense size, and forms an important weapon of offence and defence. The *second maxilliped* resembles the third, but is considerably smaller: the *first* (6) has its endopodite greatly reduced, the two segments of its protopodite large and leaf-like, and no gill is connected with the epipodite.

The head bears a pair of mandibles and two pairs of maxillæ in relation with the mouth, and in front of that aperture a pair of antennules and one of antennæ. The hindmost appendage of the head is the *second maxilla* (5), a leaf-like appendage, its protopodite being cut up into lobes, while the exopodite is modified into a boomerang-shaped plate, which by its movements produces a current of water over the gills. The *first maxilla* (4) is a very small organ, having neither exo- nor epipodite. The *mandible* (3) is a large, strongly calcified body, toothed along

its inner edge, and bearing on its anterior border a little three-jointed feeler-like body, the *palp*, the two distal segments of which represent the endopodite, its proximal segment, together with the mandible proper, the protopodite.

The *antenna* (2) is of great size, being nearly as long as the whole body. It consists of an axis of five podomeres, the fifth or last of which bears a long, flexible, many-jointed structure, or *flagellum* (*fl*), while from the second segment springs a scale-like body or *squame* (*ex*). It is fairly obvious that the two proximal segments represent the protopodite, the remaining three, with the flagellum, the endopodite, and the squame the exopodite.

The *antennule* (1) has an axis of three podomeres ending in two many-jointed flagella (*fl.* 1, *fl.* 2), which are sometimes considered as endo- and exopodite. But in all the other limbs, as we have seen, the exopodite springs from the second segment of the axis, and the probabilities are that there is no exact correspondence between the parts of the antennule and those of the remaining appendages.

The *eye-stalks*, already noticed, arise just above the antennules, and are formed each of a small proximal and a large distal segment. They are sometimes counted as appendages serially homologous with the antennæ and legs, &c., but are more properly to be looked upon as articulated processes of the prostomium. It is possible that the antennules are also prostomial and not metameric structures: assuming this to be the case, it will be seen that the body of the crayfish consists of a prostomium, eighteen metameres, and a telson, which is probably composed of an anal segment *plus* a post-anal extension. The prostomium bears eye-stalks and antennules: the first four metameres are fused with the prostomium to form the head, and bear the antennæ, mandibles, first maxillæ, and second

maxillæ: the next eight metameres (fifth—twelfth) constitute the thorax, and bear the three pairs of maxillipeds and the five pairs of legs: the remaining six metameres (thirteenth—eighteenth), together with the anal segment, constitute the abdomen, and bear five pairs of pleopods and one of uropods.

The articulation of the various podomeres of the appendages is on the same plan as that of the abdominal segments (p. 320). The podomeres are, it must be remembered, rigid tubes: they are connected with one another by flexible *articular membranes* (Fig. 85, *art. m*), but at two points the adjacent ends of the tubes come into contact with one another and are articulated by peg-and-socket joints (*h*), the two joints being at opposite ends of a diameter which forms the *axis of articulation*. The two podomeres can therefore be moved upon one another in a plane at right angles to the axis of articulation and in no other direction, the joints being pure hinge-joints. As a rule the range of movement is from the perpendicular to a tolerably extensive flexion on one side—the articulations are single-jointed, like our own elbows and knees. The whole limb is, however, capable of universal movement, owing to the fact that the axes of articulation vary in direction in successive joints: the first joint of a limb bending, for instance, up and down, the next backwards and forwards, the next obliquely, and so on. In some cases, *e.g.*, in the pleopods, peg-and-socket joints are absent, the articulation being formed merely by an annular articular membrane, movement being therefore possible in any plane.

Sections show the body-wall to consist of a layer of deric epithelium (Fig. 83, *Der. Epthm*) secreting a thick cuticle (*Cu*), a layer of connective tissue forming the dermis (*Derm*), and a very thick layer of large and complicated

muscles (*M*), which fill up a great part of the interior of the body. Neither on the deric epithelium nor elsewhere are there any cilia, the absence of these structures being generally characteristic of Arthropods.

The cuticle (*Cu*) is of great thickness, and except at the joints between the various segments of the body and limbs, is impregnated with lime-salts so as to form a hard, jointed armour. It thus constitutes a skeleton which, unlike that of the starfish (p. 310), is a cuticular exoskeleton, forming a continuous investment over the whole body but discontinuously calcified. It is shed and renewed periodically—once a year during adult life—the process being known as *ecdysis*.

The *muscular system* shows a great advance in complexity over that of Polygordius, and consists entirely of transversely striated fibres. In the abdomen the muscles are of great size, and are divisible into a smaller dorsal and a larger ventral set. The dorsal muscles (Fig. 86, *em*; Fig. 84, *d. m*) are paired longitudinal bands, divided into segments called *myomeres*, and inserted by connective tissue into the anterior border of each segment: anteriorly they are traceable into the thorax, where they arise from the side-walls of that region. When these muscles contract they draw the anterior edge of each tergum under the posterior edge of its predecessor, and thus extend or straighten the abdomen.

The ventral muscles (Fig. 86, *f m*) are extraordinarily complex. Omitting details, there is on each side a wavy longitudinal band of muscle (Fig. 84, *c.m*), nearly circular in section, which sends off a slip (*ex*) to be inserted into each segment above the hinge: the contraction of this muscle must obviously tend to approximate the terga, and so aid the dorsal muscles in extending the abdomen. Around this *central muscle* is wrapped, in each segment, a band of

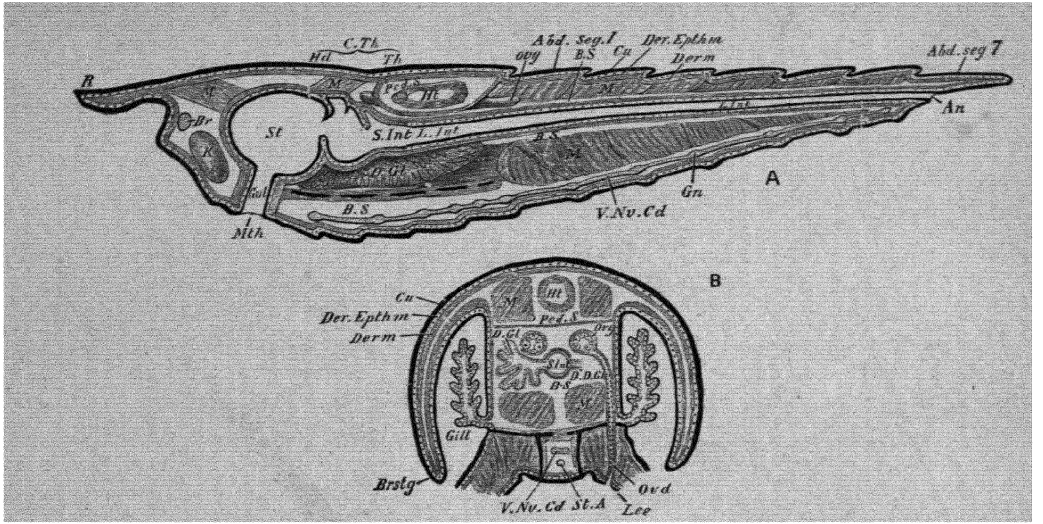

FIG. 83.—Diagrammatic sections of a Fresh-water Crayfish.

A, longitudinal section : the right digestive gland (*D. Gl*) and ovary (*Ovy*) are shown in perspective.

B, transverse section through the thorax : the digestive gland (*D. Gl*) is shown only on the left, the oviduct (*Ovd*) only on the right side.

The cuticle is black, the ectoderm coarsely dotted, the nervous system finely dotted, the endoderm radially striated, and the mesoderm evenly shaded.

The body is divided into a head (*Hd*) and thorax (*Th*), together constituting the cephalothorax (*C. Th*), and seven free abdominal segments (*Abd. seg.* 1, *Abd. seg.* 7): the head is produced in front into a rostrum (*R*).

The body-wall consists of cuticle (*Cu*), partly calcified to form the exoskeleton, deric epithelium (*Der. Epthm*), dermis (*Derm*), and a very thick layer of muscle (*M*) which in the abdomen is distinctly segmented.

The mouth (*Mth*) leads by a short gullet (*Gul*) into a large stomach (*St*), from which a short small intestine (*S. Int*) leads into a large intestine (*L. Int*), ending in the anus (*An*). Opening into the small intestine are the digestive glands (*D. Gl*). The epithelium of the small intestine and digestive glands is endodermal, that of the rest of the canal is ectodermal and secretes a cuticle: the outer layer throughout is mesodermal (connective tissue and muscle).

The cavity (*B. S*) between the enteric canal and the body-muscles is a blood-sinus.

The heart (*Ht*) is enclosed in the pericardial sinus (*Per. S*): the chief ventral blood-vessel or sternal artery (*St. A*) is shown in B.

The gills (B, *Gill*) are enclosed in a cavity formed by a fold of the thoracic body-wall called the branchiostegite (*Brstg*): they are formed of the same layers as the body-wall, of which they are offshoots.

The kidneys (A, *K*) are situated in the head.

The brain (*Br*) lies in the prostomium: the ventral nerve-cord (*V. Nv. Cd*) consists of a chain of ganglia (*Gn*) united by connectives.

The ovary (*ovy*) is a hollow organ opening by an oviduct (B, *ovd*) on the base of one of the legs (*Leg*).

muscle (*env. m*) in the form of a loop, the outer limb of which (*fl*) turns forwards and is inserted into a sternum, while the inner limb (*fl'*) turns backwards and is inserted into another and more posterior sternum. The contraction of this *enveloping muscle* produces an approximation of the sterna, and thus flexes the abdomen, the central muscle always keeping the middle of the loop in place. The ventral muscles are, like the dorsal, traceable into the thorax, where they arise from the endophragmal system: their various parts are connected by a complex system of fibres extending between the central and enveloping muscles, and connecting both with their fellows of the opposite side. The flexor muscles are immensely powerful, and produce, when acting together, a sudden and violent bending of the

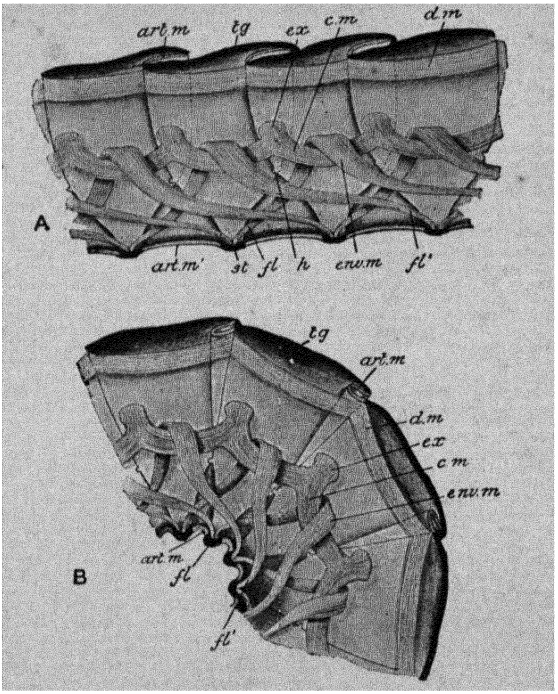

FIG. 84.—Diagram illustrating the action of the abdominal muscles in the Crayfish. A shows the position in extension, B in flexion.

Four abdominal segments are shown in sagittal section: *tg*, terga; *st*, sterna; *art. m*, tergal articular membranes; ***art. m'***, **sternal articular membranes**; *h*, hinges.

The muscles are represented as narrow bands (comp. Fig. 86 for their actual dimensions), and their arrangement is greatly simplified. *d.m*, dorsal muscles; *c.m*, central muscle giving off extensor slips (*ex*); *env. m*, enveloping muscles continued into anterior (*fl*) and posterior (*fl'*) flexor slips.

(From Parker and Haswell's *Zoology*.)

abdomen upon the cephalothorax, causing the crayfish to dart backwards with great rapidity.

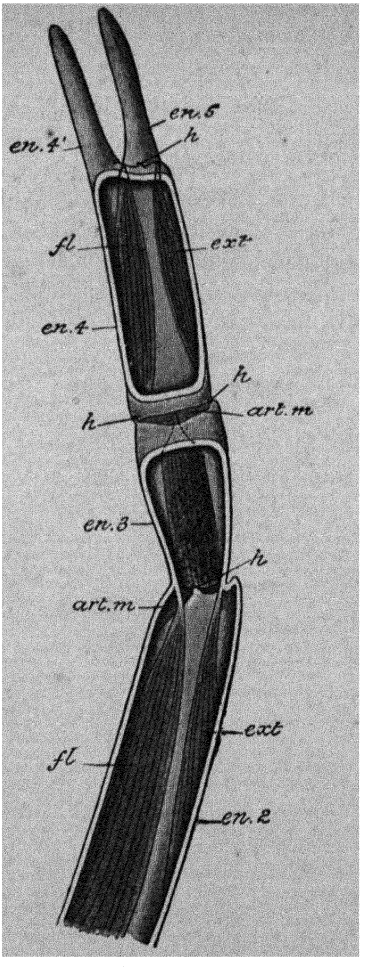

FIG. 85.—A leg of the Fresh-water Crayfish with part of the exoskeleton removed to show the muscles.

en. 2–*en.* 5, segments of endopodite ; *h*, hinges ; *art. m*, articular membrane ; *ext*, extensor muscles ; *fl*, flexor muscles.

(From Parker and Haswell's *Zoology*.)

It will be seen that the body-muscles of Astacus cannot be said to form a layer of the body-wall, as in Polygordius, but constitute an immense fleshy mass, filling up the greater part of the body-cavity, and leaving a very small space around the enteric canal.

In the limbs (Fig. 85) each podomere is acted upon by two muscles situated in the next proximal podomere. These muscles are inserted, by chitinous and often calcified tendons, into the proximal edge of the segment to be moved, the smaller (*ext*) on the extensor, the larger (*fl*) on the flexor side, in each case half-way between the two hinges, so that a line joining the two muscular insertions is at right angles to the axis of articulation.

The digestive organs are constructed on the same general plan as those of Polygordius, but present many striking differences. The *mouth* (Fig. 83, A, *Mth*) lies in the middle ventral line of the head, and is bounded in front by a shield-shaped process, the *labrum*, at the sides by the mandibles, and behind by a pair of delicate lobes, the *paragnatha*. It leads by a short wide *gullet* (Fig. 83, *Gul;* Fig. 86, *œ*) into a capacious "*stomach*," which occupies a great part of the interior of the head, and is divided into a large anterior or *cardiac division* (Fig. 83, *St;* Fig. 86, *cs*), and a small posterior or *pyloric division* (*ps*): the latter passes into a narrow and very short *small intestine* (Fig. 83, *S. Int;* Fig. 86, *md*), from which a somewhat wider *large intestine* (Fig. 83, *L. Int;* Fig. 86, *hd*) extends to the *anus* (*an*), situated on the ventral surface of the telson.

The outer layer of the enteric canal consists of connective tissue containing striped muscular fibres: within this is a single layer of columnar epithelial cells, none of them glandular. In the gullet and stomach, and in the large intestine, the epithelium secretes a layer of chitin, which

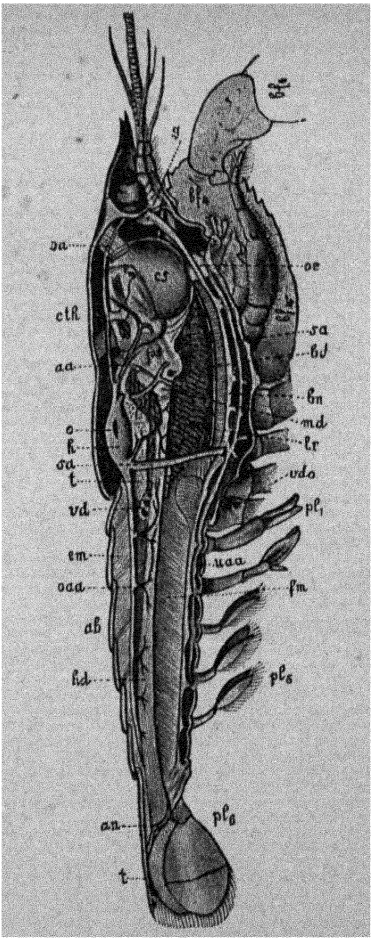

FIG 86 — Dissection of Fresh water Crayfish made by removing the exoskeleton with the appendages and the muscles, digestive gland and kidney of the right side (compare with diagram in the figure 83 A)

aa, antennary artery, *ab*, abdomen, *an*, anus, *b d*, aperture of right digestive duct exposed by removal of gland *bf* 4, cheliped *bn*, ventral nerve cord, *cs*, cardiac division of stomach, *ctk*, cephalo

thorax ; *œ*, gullet ; *em*, dorsal muscles ; *fm*, ventral muscles ; *g*, brain ; *h*, heart ; *hd*, large intestine ; *lr*, left digestive gland ; *md*, small intestine ; *o*, right lateral ostium of heart ; *oa*, ophthalmic artery ; *oaa*, dorsal abdominal artery ; *œ*, gullet ; *pl.* 1–5, pleopods ; *pl.* 6, uropod ; *ps*, pyloric division of stomach ; *s. a*, sternal artery ; *t* (near heart), testis ; *t* (below anus) telson ; *vaa*, ventral abdominal artery ; *v. d*, vas deferens ; *vdo*, male genital aperture.

(From Lang, after Huxley.)

thus constitutes the innermost layer of those cavities. It is proved by development that the small intestine, which has no chitinous lining, is the only part of the enteric canal developed from the enteron of the embryo : the gullet and stomach arise from the stomodæum, the large intestine from the proctodæum. Thus a very small portion of the enteric epithelium is endodermal (see Fig. 83, A).

In the cardiac division of the stomach the chitinous lining is thickened and calcified in certain parts, so as to form a complex articulated framework, the *gastric mill*, on which are borne a median and two lateral *teeth*, strongly calcified and projecting into the cavity of the stomach. Two pairs of strong muscles arise from the carapace, and are inserted into the stomach : when they contract they move the mill in such a way that the three teeth meet in the middle line and complete the comminution of the food begun by the jaws. The separation of the teeth is effected partly by the elasticity of the mill, partly by delicate muscles in the walls of the stomach. The pyloric division of the stomach forms a strainer : its walls are thickened and produced into numerous setæ, which extend quite across the narrow lumen and prevent the passage of any but finely divided particles into the intestine. Thus the stomach has no digestive function, but is merely a masticating and straining apparatus. On each side of the cardiac division is found, at certain seasons of the year, a plano-convex mass of calcareous matter, the *gastrolith* or "crab's-eye."

The digestion of the food, and to some extent the absorption of the digested products, are performed by a pair of large glands (Fig. 83, *D. Gl.*; Fig. 86, *hr*), lying one on each side of the stomach and anterior end of the intestine. They are formed of finger-like sacs or *cæca*, which discharge into wide ducts opening into the small intestine, and are lined with glandular epithelium derived from the endoderm of the embryo. The glands are often called livers, but as the yellow fluid they secrete digests proteids as well as fat, the name *hepato-pancreas* is often applied to them, or they may be called simply *digestive glands*. The crayfish is carnivorous, its food consisting largely of decaying animal matter.

The digestive organs and other viscera are surrounded by a body-cavity, which is in free communication with the blood-vessels and itself contains blood. This cavity is not lined by epithelium, and is to be looked upon as an immense blood-sinus, and not as a true cœlome.

There are well-developed respiratory organs in the form of *gills* (Fig. 83, B), contained in a narrow branchial chamber, bounded internally by the proper wall of the thorax, externally by the gill-cover or pleural region of the carapace. Each gill consists of a stem giving off numerous branchial filaments, so that the whole organ is plume-like. The filaments are hollow and communicate with two parallel canals in the stem—an external, the *afferent branchial vein*, and an internal, the *efferent branchial vein*. The gill is to be considered as an out-pushing of the body-wall, and contains the same layers—a thin layer of chitin externally, then a single layer of epithelial cells, and beneath this connective tissue, hollowed out for the blood channels.

According to their point of origin the gills are divisible into three sets—first, *podobranchiæ* or foot-gills (Fig. 87, A,

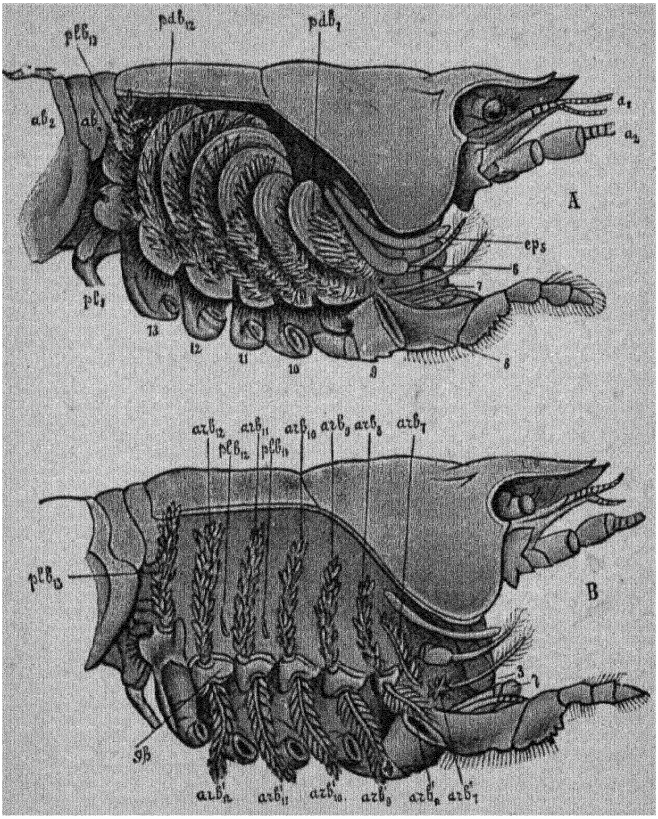

FIG. 87.—Two dissections showing the gills of the Fresh-water Crayfish.

In A the right gill-cover has been removed, but the gills are undisturbed: in B the podobranchiæ (*pdb.* in A) are cut away, and the outer set of arthrobranchiæ (*arb*[1]) turned down to show the inner arthrobranchiæ (*arb*) and the pleurobranchiæ (*plb.*).

All the gills are numbered according to the segment from which they spring, the first thoracic segment being numbered 6, the last 13.

ep. 5, scaphognathite.

ab. 1, *ab.* 2, abdominal segments; a^1, antennule; a^2, antenna; 6-8, maxillipeds; 9-13, legs; *pl.* 1, first pleopod.

(From Lang, after Huxley.)

pdb), springing from the epipodites of the thoracic appendages, from which they are only partially separable; secondly, *arthrobranchiæ* or joint-gills (B, *arb*), springing from the articular membranes connecting the thoracic appendages with the trunk; and thirdly, *pleurobranchiæ*, or wall-gills (*plb*), springing from the lateral walls of the thorax, above the attachment of the appendages. The total number of gills is eighteen, besides two filaments representing vestigial or vanishing gills.

The *excretory organs* differ both in position and in form from those of Polygordius. There are no distinct nephridia, but at the base of each antenna is an organ of a greenish colour, the *antennary* or *green gland* (Fig. 83, A, *K*), by which the function of renal excretion is performed. The gland is cushion-shaped, and contains canals and irregular spaces lined by glandular epithelium: it discharges its secretion into a thin-walled sac or *urinary bladder*, which opens by a duct on the proximal segment of the antenna. The green glands are to be looked upon as organs of the same general nature as nephridia.

The *circulatory organs* are in a high state of development. The *heart* (Fig. 83, *IIt*; Fig. 86, *h*) is situated in the dorsal region of the thorax, and is a roughly polygonal muscular organ pierced by three pairs of apertures or *ostia* (Fig. 86, *o*), guarded by valves which open inwards. It is enclosed in a spacious *pericardial sinus* (Fig. 83, *Pcd. S*), which contains blood. From the heart spring a number of narrow tubes, called *arteries*, which serve to convey the blood to various parts of the body. At the origin of each artery from the heart are valves which allow of the flow of blood in one direction only, *viz.*, from the heart to the artery. From the anterior end of the heart arise five vessels — a median *ophthalmic artery* (Fig. 86, *oa*), which passes forwards to the

eyes; paired *antennary arteries* (*aa*), going to the antennules, antennæ, green glands, &c., and sending off branches to the stomach; and paired *hepatic arteries*, going to the digestive glands. The posterior end of the heart gives off two unpaired arteries practically united at their origin, the *dorsal abdominal artery* (*oaa*), which passes backwards above the intestine, sending branches to it and to the dorsal muscles; and the large *sternal artery* (*sa*), which passes directly downwards, indifferently to right or left of the intestine, passing between the connectives uniting the third and fourth thoracic ganglia, and then turns forwards and runs in the sternal canal, immediately beneath the nerve-cord, and sends off branches to the legs, jaws, &c. At the point where the sternal artery turns forwards it gives off the median *ventral abdominal artery* (*v. a. a*), which passes backwards beneath the nerve-cord, and supplies the ventral muscles, pleopods, &c.

All these arteries branch extensively in the various organs they supply, becoming divided into smaller and smaller offshoots, which finally end in microscopic vessels called *capillaries*. These latter end by open mouths which communicate with the *blood-sinuses*, spacious cavities lying among the muscles and viscera, and all communicating sooner or later with the *sternal sinus* (Fig. 83, A, *B. S*), a great median canal running longitudinally along the thorax and abdomen, and containing the ventral nerve-cord and the sternal and ventral abdominal arteries. In the thorax the sternal sinus (Fig. 88, *st. s*) sends an offshoot to each gill in the form of a well-defined vessel, which passes up the outer side of the gill and is called the *afferent branchial vein* (*af. br. v*). Spaces in the gill-filaments place the afferent in communication with the *efferent branchial vein* (*ef. br. v*), which occupies the inner side of the gill-

stem. The eighteen efferent branchial veins open into six *branchio-cardiac veins* (*br. c. v*), which pass dorsally in close contact with the lateral wall of the thorax and open into the pericardial sinus.

The whole of this system of cavities is full of blood, and the heart is rhythmically contractile. When it contracts the blood contained in it is prevented from entering the pericardial sinus by the closure of the valves of the ostia, and therefore takes the only other course open to it, *viz.*, into the arteries. When the heart relaxes, the blood in the arteries is prevented from regurgitating by the valves at their origins, and the pressure of blood in the pericardial sinus forces open the valves of the ostia and so fills the heart. Thus in virtue of the successive contractions of the heart, and of the disposition of the valves, the blood is kept constantly moving in one direction, *viz.*, from the heart by the arteries to the various organs of the body, where it receives carbonic acid and other waste matters; thence by sinuses into the great sternal sinus; from the sternal sinus by afferent branchial veins to the gills, where it exchanges carbonic acid for oxygen; from the gills by efferent branchial veins to the branchio-cardiac veins, thence into the pericardial sinus, and so to the heart once more.

It will be seen that the circulatory system of the crayfish consists of three sections—(1) the *heart* or organ of propulsion; (2) a system of out-going channels, the *arteries*, which carry the blood from the heart to the body generally; and (3) a system of returning channels—some of them, the *sinuses*, mere irregular cavities, others, the *veins*, with definite walls—these return the blood from the various organs back to the heart. The respiratory organs, it should be observed, are interposed in the returning current, so that blood is taken both to and from the gills by veins.

Comparing the blood-vessels of Astacus with those of Polygordius, it would seem that the ophthalmic artery, heart, and dorsal abdominal artery together answer to the dorsal vessel, part of which has become enlarged and muscular, and discharges the whole function of propelling the

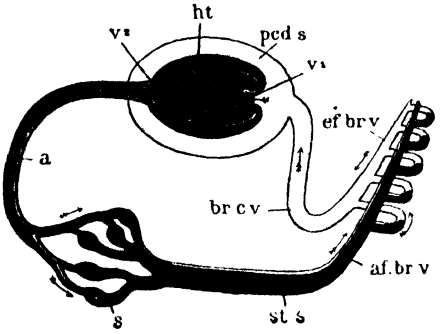

FIG. 88.—Diagram illustrating the course of the circulation of the blood in the Crayfish.

Heart and arteries red: veins and sinuses containing non-aerated blood blue: veins and sinuses containing aerated blood pink.

The arrows show the direction of the flow.

The blood from the pericardial sinus (*pcd. s*) enters the heart (*ht*) by a valvular aperture (v^1) and is propelled into arteries (*a*), the orifices of which are guarded by valves (v^2): the ultimate branches of the arteries discharge the blood into sinuses (*s*), and the sinuses in various parts of the body debouch into the sternal sinus (*st. s*): thence the blood is taken by the afferent branchial veins (*af. br. v*) into the gills, where it is purified and is returned by efferent branchial veins (*ef. br. v*) into the branchio-cardiac veins (*br. c. v*) which open into the pericardial sinus.

(From Parker and Haswell's *Zoology*.)

blood. The horizontal portion of the sternal artery, together with the ventral abdominal, represent the ventral vessel, while the vertical portion of the sternal artery is a commissure, developed sometimes on the right, sometimes on the left side, its fellow being suppressed.

The blood when first drawn is colourless, but after exposure to the air takes on a bluish-gray tint. This is owing to the presence of a colouring matter called *hæmocyanin*, which becomes blue when combined with oxygen; it is a respiratory pigment, and serves, like hæmoglobin, as a carrier of oxygen from the external medium to the tissues. The hæmocyanin is contained in the plasma of the blood: the corpuscles are all leucocytes.

The *nervous system* consists, like that of Polygordius, of a brain (Fig. 86, *g*) and a ventral nerve-cord (*bn*), united by œsophageal connectives. But the ventral nerve-cord is differentiated into a series of paired swellings or *ganglia* to which the nerve-cells are confined, united by longitudinal connectives. The brain supplies not only the eyes and antennules, but the antennæ as well, and it is found by development that the two pairs of ganglia belonging to the antennulary and antennary segments have fused with the brain proper. Hence we have to distinguish between a primary brain or *archi-cerebrum*, the ganglion of the prostomium, and a secondary brain or *syn-cerebrum* formed by the union of one or more pairs of ganglia of the ventral cord with the archi-cerebrum. A further case of concrescence of ganglia is seen in the ventral nerve-cord, where the ganglia of the last three cephalic and first three thoracic segments have united to form a large compound *sub-œsophageal ganglion*. All the remaining segments have their own ganglia, with the exception of the telson, which is supplied from the ganglion of the preceding segment. There is a *visceral system* of nerves supplying the stomach, originating in part from the brain and in part from the œsophageal connectives.

The eyes have a very complex structure. The chitinous cuticle covering the distal end of the eye-stalk is transparent,

divided by delicate lines into square areas or *facets*, and constitutes the *cornea*. Beneath each facet of the cornea is an apparatus called an *ommatideum*, consisting of an outer segment or *vitreous body* having a refractive function, and an inner segment or *retinula* forming the actual visual portion of the apparatus. The ommatidia are optically separated from one another by black pigment, so that each is a distinct organ of sight, and the entire eye is called a compound eye.

The antennules contain two sensory organs, to which are usually assigned the functions of smell and hearing respectively. The "*olfactory*" *organ* is constituted by a number of delicate *olfactory setæ*, borne on the external flagellum and supplied by the antennulary nerve. The "*auditory*" *organ* or *statocyst* is a sac formed by invagination of the dorsal surface of the proximal segment, and is in free communication with the surrounding water by a small aperture. The chitinous lining of the sac is produced into delicate feathered *auditory setæ*, supplied by branches of the antennulary nerve, and in the water which fills the sac are minute sand-grains, which take the place of the otoliths or ear-stones found in most auditory organs, but which, instead of being formed by the animal itself, are taken in after each ecdysis, when the lining of the sac is shed. Many of the setæ on the general surface of the body have a definite nerve-supply, and are probably *tactile organs*.

The crayfish is diœcious, and presents a very obvious sexual dimorphism or structural difference between male and female, apart from the actual organs of reproduction. The abdomen of the female is much broader than that of the male: the first and second pleopods of the male are modified into tubular or rather spout-like copulatory organs; and the reproductive aperture is situated in the male on the

proximal podomere of the fifth leg, in the female on that of the third.

The *spermary* (Fig. 86, *t*) lies in the thorax, just beneath the floor of the pericardial sinus, and consists of paired anterior lobes and an unpaired posterior lobe. From each side goes off a convoluted *spermiduct* or *vas deferens* (*vd*), which opens on the proximal segment of the last leg. The sperms are curious non-motile bodies produced into a number of stiff processes: they are aggregated into vermicelli-like *spermatophores* by a secretion of the vas deferens.

The *ovary* is also a three-lobed body, and is similarly situated to the testis: from each side proceeds a thin-walled *oviduct*, which passes downwards, without convolutions, to open on the proximal segment of the third or antepenultimate leg. The eggs are of considerable size and contain a great quantity of yolk (*see* p. 256).

Both ovary and testis are hollow organs, discharging their products internally. Their cavities represent the cœlome, and their ducts are organs of the same general nature as nephridia. The ova, when laid, are fastened to the setæ on the pleopods of the female by the sticky secretion of glands occurring both on those appendages and on the segments themselves: they are fertilised immediately after laying, the male depositing spermatophores on the ventral surface of the female's body just before oviposition.

The process of segmentation of the oosperm presents certain striking peculiarities. The nucleus divides repeatedly (Fig. 89, A, *nu*), but no corresponding division of the protoplasm takes place, with the result that the morula-stage, instead of being a heap of cells, is simply a multinucleate but non-cellular body. Soon the nuclei thus formed retreat from the centre of the embryo, and arrange themselves in a single layer close to the surface (B): around each of these

protoplasm accumulates, the central part of the embryo consisting entirely of yolk material. We thus get a *superficial segmentation*, characterised by a central mass of yolk and a superficial layer of cells collectively known as the *blastoderm* (C).

On one pole an invagination of the blastoderm takes place, giving rise to a small sac, the enteron, which communicates with the exterior by an aperture, the blastopore. By this process the embryo passes into the gastrula-stage, which, however, differs from the corresponding stage in Polygordius

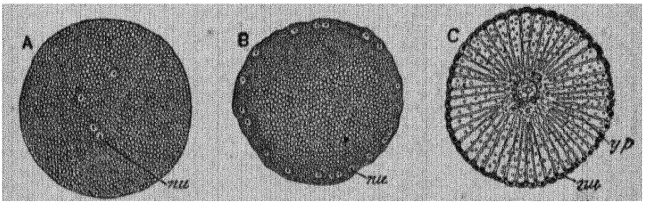

FIG. 89.—Three stages in the early development of the Crayfish.

In A the products of division of the nucleus (*nu*) are seen in the centre of the yolk: in B and C the nuclei have arranged themselves in a peripheral layer, each surrounded by protoplasm, so as to form the blastoderm.

(From Parker and Haswell's *Zoology*, after Morin.)

(p. 295) in the immense quantity of food-yolk filling up the space (blastocœle) between ectoderm and endoderm. Very soon the embryo becomes triploblastic, or three-layered, by the budding off of cells from the endoderm in the neighbourhood of the blastopore: these accumulate between the ectoderm and endoderm, and constitute the mesoderm.

Before long the blastopore closes, and a stomodæum and proctodæum (p. 296) are formed as invaginations of the ectoderm which eventually communicate with the enteron, forming a complete enteric canal. On each side of the mouth

or aperture of the stomodæal depression (Fig. 90) three elevations appear, the rudiments of the antennules (a^1), antennæ (a^2), and mandibles (m): in front of them is another pair of elevations on which the eyes (A) subsequently appear.

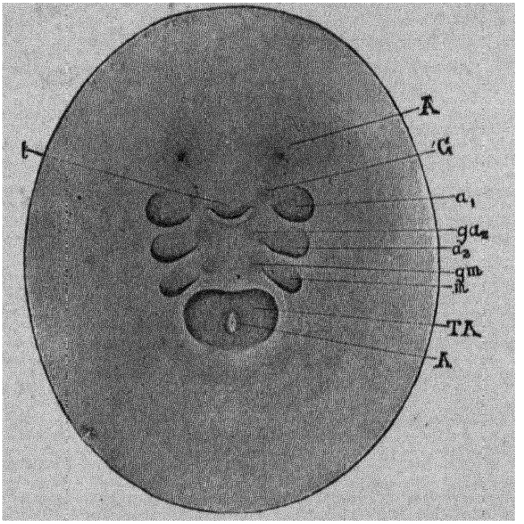

FIG. 90.—Early embryo of Fresh-water Crayfish in the nauplius stage.

A in the upper part of the figure is the eye: *l*, the labrum overhanging the mouth, on each side of which are the rudiments of the antennules (a^1), antennæ (a^2), and mandibles (m): behind them is the rudiment of the thorax and abdomen (TA) with the anus (A). The rudiments of the first three pairs of ganglia (G, ga^2, gm) are seen through the transparent ectoderm.

(From Lang, after Reichenbach.)

An unpaired elevation (TA) behind the mouth, and having the anus (A) or aperture of the proctodæal depression at its summit, is the rudiment of the thorax and abdomen. The embryo is now called a ***nauplius***. Many Crustacea are

hatched in the form of a free swimming larva, to which this name is applied, characterised by the presence of three pairs of appendages, used for swimming and becoming the

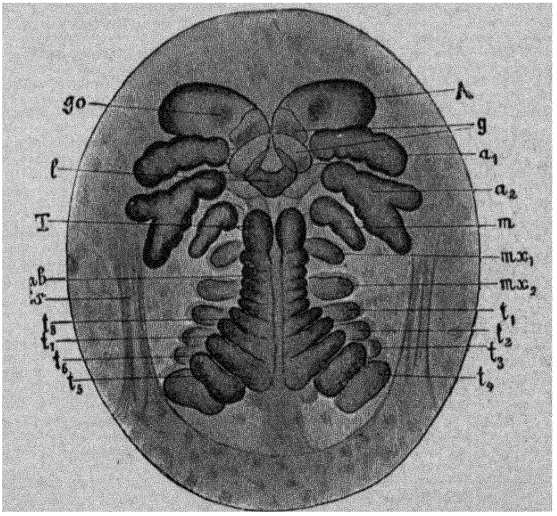

FIG. 91.—**Later embryo of Fresh-water** Crayfish, from the ventral aspect; the abdomen (*ab*) is folded down over the cephalothorax, so that its dorsal surface faces the observer, and the telson (*T*) reaches nearly to the mouth.

The following appendages are indicated: A, eye-stalks; a^1, antennules; a^2, antennæ; *m*, mandibles; mx^1, mx^2, maxillæ; *t*. 1–*t*. 8, thoracic appendages (maxillipedes and legs).

At the sides of the thorax are seen the edges of the carapace (*ts*): in front of the mouth is the labrum (*l*), in front of the labrum the brain (*g*), and at the base of the eye-stalk the optic ganglion (*go*).

(From Lang, after Reichenbach.)

antennules, antennæ, and mandibles of the adult. In the crayfish there is no free larva, and the nauplius stage is passed through before hatching.

The nauplius is gradually transformed into the crayfish by

the appearance of fresh appendages, in regular order, behind the first three (Fig. 91); by the elongation of the rudiment of thorax and abdomen (*ab*); and by the gradual differentiation of the appendages. When hatched the young animal agrees in all essential respects with the adult, but its proportions are very different, the cephalothorax being nearly globular and the abdomen small. For some time after hatching the young crayfishes cling in great numbers to the pleopods of the mother by means of the peculiarly hooked chelæ of the first pair of legs.

LESSON XXVIII

THE FRESH-WATER MUSSEL

In the mussel we meet with an entirely new type of structure: the animal is bilaterally symmetrical, with no trace of metameric segmentation; the power of locomotion is greatly restricted, and food is obtained passively by ciliary action, as in Infusoria, not by the active movements of definite seizing organs—tentacles, limbs, or protrusible mouth—as in most of the higher animal forms.

Fresh-water mussels are found in rivers and lakes in most parts of the world. *Anodonta cygnea*, the swan-mussel, is the commonest species in England; but the pearl-mussel, *Unio margaritifer*, is found in mountain streams, and other species of the same genus are universally distributed.

The mussel is enclosed in a brown shell formed of two separate halves or *valves* hinged together along one edge. It lies on the bottom, partly buried in the mud or sand, with the valves slightly gaping, and in the narrow cleft thus formed a delicate, semi-transparent substance is seen, the edge of the *mantle* or *pallium*. The mantle really consists of separate halves or *lobes* corresponding with the valves of

the shell, but in the position of rest the two lobes are so closely approximated as to appear simply like a membrane uniting the valves. At one end, however, the mantle projects between the valves in the form of two short tubes, one (Fig. 92, B, *ex. sph.*) smooth-walled, the other (*in. sph.*) beset with delicate processes or *fimbriæ*. By diffusing particles of carmine or indigo in the water it can be seen that a current is always passing in at the fimbriated tube, hence called the *inhalant siphon*, and out at the smooth or *exhalant siphon*. Frequently a semi-transparent, tongue-like body (*ft*) is protruded between the valves at the opposite side from the hinge and at the end furthest from the siphons: this is the *foot*, by its means the animal is able slowly to plough its way through the sand or mud. When irritated the foot and siphons are withdrawn and the valves tightly closed. In a dead animal, on the other hand, the shell always gapes, and it can then be seen that each valve is lined by the corresponding lobe of the mantle, that the exhalant siphon is formed by the union of the lobes above and below it and is thus an actual tube, but that the boundary of the inhalant siphon facing the gape of the shell is simply formed by the approximation of the mantle-lobes, so that this tube is a temporary one.

The hinge of the shell is dorsal, the gape ventral, the end bearing the siphons posterior, the end from which the foot is protruded anterior: hence the valves and mantle-lobes are respectively right and left.

In a dead and gaping mussel the general disposition of the parts of the animal is readily seen. The main part of the body lies between the dorsal ends of the valves: it is produced in the middle ventral line into the keel-like foot: and on each side, between the foot and the corresponding mantle-lobe, are two delicate, striated plates, the *gills*. Thus

the whole animal has been compared to a book, the back being represented by the hinge, the covers by the valves, the fly-leaves by the mantle-lobes, the two first and the two last pages by the gills, and the remainder of the leaves by the foot.

When the body of the mussel is removed from the shell the two valves are seen to be united, along a straight *hinge-line* (Fig. 92, A, *h. l*), by a tough, elastic substance, the *hinge-ligament* (Fig. 93, B, *lig*) passing transversely from valve to valve. It is by the elasticity of this ligament that the shell is opened: it is closed, as we shall see, by muscular action: hence the mere relaxation of the muscles opens the shell. In Anodonta the only junction between the two valves is afforded by the ligament, but in Unio each is produced into strong projections and ridges, the *hinge-teeth*, separated by grooves or sockets, and so arranged that the teeth of one valve fit into the sockets of the other.

The valves are marked externally by a series of concentric lines parallel with the free edge or gape, and starting from a swollen knob or elevation, the *umbo*, situated towards the anterior end of the hinge-line. These lines are *lines of growth*. The shell is thickest at the umbo, which represents the part originally formed, and new layers are deposited under this original portion, as secretions from the mantle, the shell being, like the armour of the crayfish, a cuticular exoskeleton. As the animal grows each layer projects beyond its predecessor, and in this way successive outcrops are produced giving rise to the markings in question. In the region of the umbo the shell is usually more or less eroded by the action of the carbonic acid in the water.

The inner surface of the shell also presents characteristic markings (Fig. 92, A). Parallel with the gape, and at a

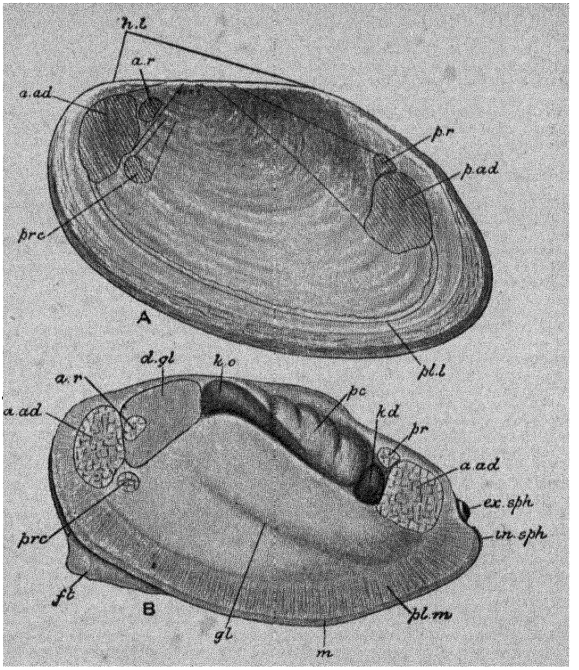

FIG. 92.—A, interior of right valve of Anodonta, showing the various impressions produced by the muscles shown in B: *h. l*, hinge-line; *pl. l.* pallial line.

B, the animal removed from the shell and seen from the left side.

a. ad, anterior adductor; *a. r*, anterior retractor; *d. g*, digestive gland, seen through mantle; *ex. sph*, exhalant siphon; *ft*, foot; *gl*, gills, seen through mantle; *in. sph*, inhalant siphon; *kd*, kidney, seen through mantle; *k. o*, Keber's organ, seen through mantle; *m*, mantle; *p. ad*, posterior adductor; *pc*, pericardium, seen through mantle; *pl. m*, pallial muscles; *p. r*, posterior retractor; *prc*, protractor.

(From Parker and Haswell's *Zoology*.)

short distance from it, is a delicate streak (*pl. l*) caused by the insertion into the shell of muscular fibres from the edge of the mantle: the streak is hence called the *pallial line*.

Beneath the anterior end of the hinge the pallial line ends in an oval mark, the *anterior adductor impression* (*a. ad*), into which is inserted one of the muscles which close the shell. A similar, but larger, *posterior adductor impression* (*p. ad*) lies beneath the posterior end of the hinge. Two smaller markings in close relation with the anterior adductor impression mark the origin of the *anterior retractor* (*a. r*), and of the *protractor* (*prc*) of the foot: one connected with the posterior adductor impression, that of the *posterior retractor* (*p. r*) muscle. From all these impressions faint converging lines can be traced to the umbo: they mark the gradual shifting of the muscles during the growth of the animal.

The shell consists of three layers. Outside is a brown horn-like layer, the *periostracum*, composed of *conchiolin*, a substance allied in composition to chitin. Beneath this is a *prismatic layer* formed of minute prisms of calcium carbonate, separated by thin layers of conchiolin; and, lastly, forming the internal part of the shell is the *nacre*, or "mother-of-pearl," formed of alternate layers of carbonate of lime and conchiolin arranged parallel to the surface. The periostracum and the prismatic layer are secreted from the edge of the mantle only, the pearly layer from the whole of its outer surface. The hinge-ligament is continuous with the periostracum, and is to be looked upon simply as a median uncalcified portion of the shell, which is therefore, in strictness, a single continuous structure.

By the removal of the shell the body of the animal (Fig. 92, B) is seen to be elongated from before backwards, narrow from side to side, produced on each side into a mantle-lobe (*m*), and continued ventrally into a keel-like *visceral mass*, which passes below and in front into the foot (*ft*). Thus each valve of the shell is in contact with

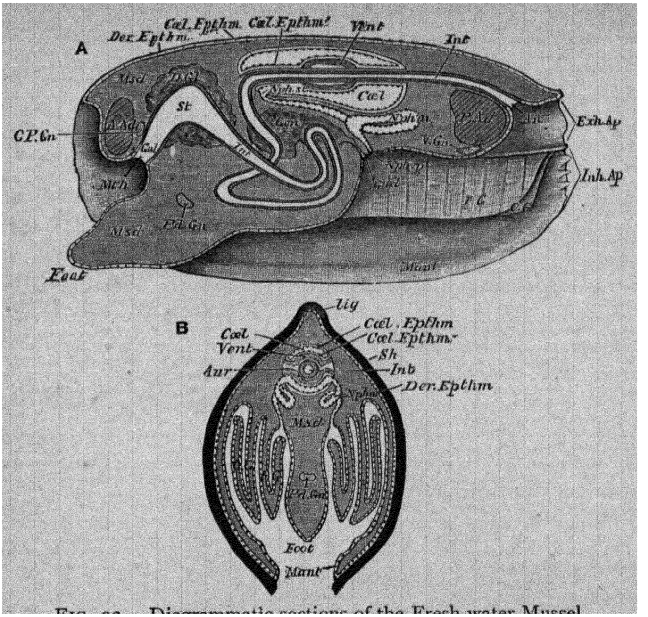

FIG. 93.—Diagrammatic sections of the Fresh-water Mussel.

A, longitudinal section: right mantle-lobe (*Mant*) and gills (*I. G*, *O. G*) are shown in perspective.

B, transverse section.

The cuticular shell (*Sh*), shown only in B, is black, the ectoderm dotted, the nervous system finely dotted, the endoderm radially striated, the mesoderm evenly shaded, and the cœlomic epithelium represented by a beaded line.

The dorsal region is produced into the right and left mantle-lobes (*Mant*), attached to which are the valves of the shell (*Sh*) joined dorsally by an elastic ligament (*lig*).

The mantle-lobes are partly united so as to form the inhalant (*Inh. Ap*) and exhalant (*Exh. Ap*) apertures at the posterior end.

The body is produced ventrally into the foot (*Foot*), on each side of which are the gills, an inner (*I. G*) and an outer (*O. G*), each formed of an inner and an outer lamella.

The body is covered externally by deric epithelium (*Der. Epthm*), within which is mesoderm (*Msd*) largely differentiated into muscles, of which the anterior (*A. Ad*) and posterior (*P. Ad*) adductors are indicated in A.

The mouth (*Mth*) leads by the short gullet (*Gul*) into the stomach (*St*), from which proceeds the coiled intestine (*Int*), ending in the anus

(*An*) : the enteric epithelium is mostly endodermal. The digestive gland (*D. Gl*) surrounds the stomach. The cœlome (*Cœl*) is reduced to a small dorsal chamber enclosing part of the intestine and the heart ; the parietal (*Cœl. Epthm*) and visceral (*Cœl. Epthm*^{1}) layers of cœlomic epithelium are shown.

The heart consists of a median ventricle (*Vent*), enclosing part of the intestine, and of paired auricles (*Aur*).

The paired nephridia (*Nphm*) open by apertures into the cœlome (*Nph. st*) and on the exterior (*Nph. p*).

The gonads (*Gon*) are imbedded in the solid mesoderm, and open on the exterior by gonoducts (*Gnd*).

The nervous system consists of a pair of cerebro-pleural ganglia (*C. P. Gn*) above the gullet, a pair of pedal ganglia (*Pd. Gn*) in the foot, and a pair of visceral ganglia (*V. Gn*) below the posterior adductor muscle.

the dorso-lateral region of the body of its own side, together with the corresponding mantle-lobe, and it is from the epithelium (Fig. 93, *Der. Epthm*) covering these parts that the shell is formed as a cuticular secretion. The whole space between the two mantle-lobes, containing the gills, visceral mass, and foot is called the *mantle-cavity*.

A single layer of epithelial cells, the deric epithelium or epidermis (*Der. Epthm*), covers the whole external surface, *i.e.*, the body proper, both surfaces of the mantle, the gills, and foot; that of the gills and the inner surface of the mantle is ciliated. Beneath the epidermis come connective and muscular tissue, which occupy nearly the whole of the interior of the body not taken up by the viscera, the cœlome being, as we shall see, much reduced. The muscles are all unstriped, and are arranged in distinct bands or sheets, many of them very large and conspicuous. The largest are the *anterior* and *posterior adductors* (Figs. 92, 93, and 94, *a. ad, p. ad*), great cylindrical muscles which pass transversely across the body and are inserted at either end into the valves of the shell, which are approximated by their contraction. Two muscles of much smaller size pass from the foot to the shell, which they serve to draw back : they

are called the *anterior* (*a. r*) and *posterior* (*p. r*) *retractors*. A third muscle (*prc*) is inserted into the shell close to the anterior adductor, and has its fibres spread fan-wise over the visceral mass which it serves to compress, thus forcing out the foot and acting as a *protractor* of that organ. The substance of the foot itself consists of a complex mass of fibres, the *intrinsic muscles* of the foot, many of which also act as protractors. Lastly, all along the border of the mantle is a row of delicate *pallial muscles* (Fig. 92, B, *pl. m*), which, by their insertion into the shell, give rise to the pallial line already seen.

The cœlome is reduced to a single ovoidal chamber, the *pericardium* (Fig. 93, *Cœl;* Fig. 94, *pc*), lying in the dorsal region of the body and containing the heart and part of the intestine: it is lined by cœlomic epithelium (*Cœl. Epthm*), and does not correspond with the pericardial sinus of the crayfish, which is a blood-space. In the remainder of the body the space between the ectoderm and the viscera is filled by the muscles and connective tissue.

The *mouth* (Fig. 94, *mth*) lies in the middle line, just below the anterior adductor. On each side of it are two triangular flaps, the internal and external *labial palps;* the external palps unite with one another in front of the mouth, forming an upper lip; the internal are similarly united behind the mouth, forming a lower lip: both are ciliated externally. The mouth leads by a short *gullet* (Fig. 94, *gul*) into a large *stomach* (*st*), which receives the ducts of a pair of irregular, dark-brown *digestive glands* (*d. gl*). The *intestine* (*int*) goes off from the posterior end of the stomach, descends into the visceral mass, where it is coiled upon itself, then ascends parallel to its first portion, turns sharply backwards, and proceeds, as the *rectum* (*rct*), through the pericardium, where it traverses the ventricle of the heart,

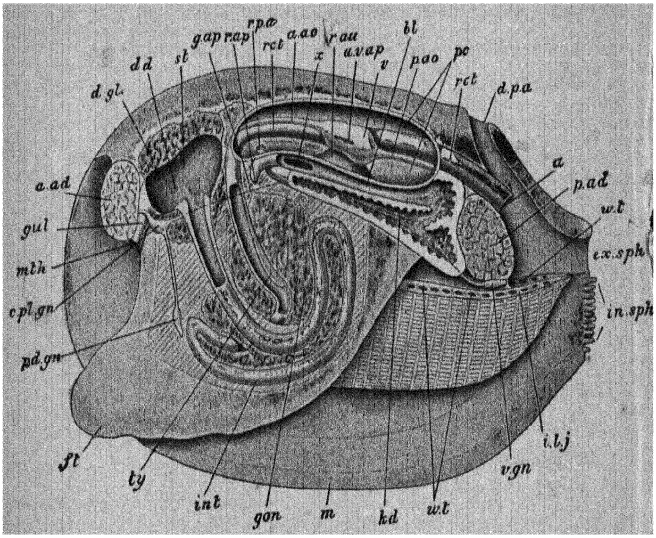

FIG. 94.—Dissection of Anodonta, made by removing the mantle-lobe, inner and outer gills, wall of pericardium, and auricle of the left side, and dissecting away the skin, muscles, &c. of the same side down to the level of the enteric canal, kidney, nervous system, &c. Part of the enteric canal is laid open, as also are the kidney (*kd*) and bladder (*bl*). The connection between the cerebro-pleural (*c. pl. gn*) and visceral (*v. gn*) ganglia is indicated by a dotted line.

a, anus; *a. ad*, anterior adductor; *a. ao*, anterior aorta; *a. v. ap*, auriculo-ventricular aperture; *bl*, urinary bladder; *c. pl. gn*, cerebro-pleural ganglion: *d. d*, duct of digestive gland; *d. gl*, digestive gland; *d. p. a*, dorsal pallial aperture; *ex. sph*, exhalant siphon; *ft*, foot; *g. ap*, genital aperture; *gon*, gonad; *gul*, gullet; *i. l. j*, inter-lamellar junction; *in. sph*, inhalant siphon; *int*, intestine; *kd*, kidney; *m*, mantle; *mth*, mouth; *p. ao*, posterior aorta; *p. ad*, posterior adductor; *pc*, pericardium; *pd. gn*, pedal ganglion; *r. ap*, renal aperture; *r. au*, right auricle; *rct*, rectum; *r. p. a*, reno-pericardial aperture; *st*, stomach; *ty*, typhlosole; *v*, ventricle; *v. gn*, visceral ganglion; *w. t*, water-tubes; *x*, aperture between right and left urinary bladders.

(From Parker and Haswell's *Zoology*.)

and above the posterior adductor, finally discharging by the *anus* (*a*) into the exhalant siphon, or cloaca. The wall of

the rectum is produced into a longitudinal ridge, or *typhlosole* (*ty*), and two similar ridges begin in the stomach and are continued into the first portion of the intestine. The stomach contains at certain seasons of the year a gelatinous rod, the *crystalline style*.

The gills consist, as we have seen, of two plate-like bodies on each side between the visceral mass and the mantle: we have thus a *right* and a *left outer* (Fig. 93, B, *O. G*), and a *right* and a *left inner gill* (*I. G*). Seen from the surface (Fig. 94), each gill presents a delicate double striation, being marked by faint lines running parallel with, and by more pronounced lines running at right angles to, the long axis of the organ. Moreover, each gill is double, being formed of two similar plates, the *inner* and *outer lamellæ*, united with one another along the anterior, ventral, and posterior edges of the gill, but free dorsally. The gill has thus the form of a long and extremely shallow bag open above (Figs. 94 and 95): its cavity is subdivided by vertical plates of tissue, the *inter-lamellar junctions* (Fig. 95, *i. l. j*), which extend between the two lamellæ and divide the intervening space into distinct compartments or *water-tubes* (*w. t*), closed ventrally, but freely open along the dorsal edge of the gill. The vertical striation of the gill is due to the fact that each lamella is made up of a number of close-set *gill-filaments* (*f*): the longitudinal striation to the circumstance that these filaments are connected by horizontal bars, the *inter-filamentar junctions* (*i. f. j*). At the thin free or ventral edge of the gill the filaments of the two lamellæ are continuous with one another, so that each gill has actually a single set of V-shaped filaments, the outer limbs of which go to form the outer lamella, their inner limbs the inner lamella. Between the filaments, and bounded above and below by the inter-filamentar junctions are minute apertures,

or *ostia* (*os*), which lead from the mantle-cavity through a more or less irregular series of cavities into the interior of the water-tubes. The filaments themselves are supported by chitinous rods, and covered with ciliated epithelium, the large cilia of which produce a current running from the exterior through the ostia into the water-tubes, and finally

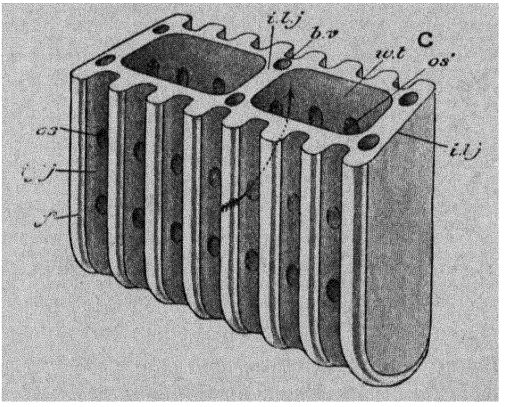

FIG. 95.—Diagram of the structure of the gill of Anodonta.
The gill is made up of V-shaped gill-filaments (*f*) arranged in longitudinal series and bound together by horizontal inter-filamentar junctions (*i. f. j*) which cross them at right angles, forming a kind of basket-work with apertures, the ostia (*os*), leading from the outside and opening (*os'*) into the cavity of the gill. The latter is divided by vertical partitions, the inter-lamellar junctions (*i. l. j*), into compartments or water-tubes (*w. t*) which open also into the supra-branchial chamber; *b. v*, blood-vessels.
(From Parker and Haswell's *Zoology*.)

escaping by the wide dorsal apertures of the latter. The whole organ is traversed by blood-vessels (*b. v*).

The mode of attachment of the gills presents certain features of importance. The outer lamella of the outer gill is attached along its whole length to the mantle: the inner

lamella of the outer, and the outer lamella of the inner gill are attached together to the sides of the visceral mass a little below the origin of the mantle: the inner lamella of the inner gill is also attached to the visceral mass in front, but is free further back. The gills are longer than the visceral mass, and project behind it, below the posterior adductor (Fig. 94), as far as the posterior edge of the mantle: in this region the inner lamellæ of the inner gills are united with one another, and the dorsal edges of all four gills constitute a horizontal partition between the pallial cavity below and the exhalant chamber or cloaca above. Owing to this arrangement it will be seen that the water-tubes all open dorsally into a *supra-branchial chamber*, continuous posteriorly with the cloaca and thus opening on the exterior by the exhalant siphon.

The physiological importance of the gills will now be obvious. By the action of their cilia a current is produced which sets in through the inhalant siphon into the pallial cavity, through the ostia into the water-tubes, thence into the supra-branchial chamber, and out at the exhalant siphon. The in-going current carries with it not only oxygen for the aëration of the blood, but also diatoms, infusoria, and other microscopic organisms, which are swept into the mouth by the cilia covering the labial palps. The out-going current carries with it the various products of excretion and the fæces passed into the cloaca. The action of the gills in producing the food-current is of more importance than their respiratory function, which they share with the mantle.

The excretory organs are a single pair of curiously-modified *nephridia*, situated one on each side of the body just below the pericardium. Each nephridium consists of two parts, a brown spongy *glandular portion* or *kidney* (Fig. 94, *kd*), and a thin-walled non-glandular part or *bladder* (*bl*). The two

parts lie parallel to one another, the bladder being placed dorsally and immediately below the floor of the pericardium: they communicate with one another posteriorly, while in front the kidney opens into the pericardium (*r. p. ap*), and the bladder on the exterior by a minute aperture (*r. ap*), situated between the inner gill and the visceral mass. Thus the whole organ (Fig. 93, *Nphm*), often called after its discoverer, the *organ of Bojanus*, is simply a tube bent upon itself, opening at one end into the cœlome (*Nph. st*), and at the other on the external surface of the body (*Nph. p*): it has therefore the normal relations of a nephridium. The epithelium of the bladder is ciliated, and produces an outward current.

It seems probable that an excretory function is also discharged by a large glandular mass of reddish-brown colour, called the *pericardial gland* or *Keber's organ* (Fig. 92, B, *k. o*). It lies in the anterior region of the body just in front of the pericardium, into which it discharges.

The circulatory system is well developed. The *heart* lies in the pericardium, and consists of a single *ventricle* (Fig. 93, *Vent*, and Figs. 94 and 96, *v*) and of right and left *auricles* (*au*). The ventricle is a muscular chamber which has the peculiarity of surrounding the rectum (Figs. 93 and 94): the auricles are thin-walled chambers communicating with the ventricle by valvular apertures opening towards the latter. From each end of the ventricle an artery is given off, the *anterior aorta* (Fig. 94, *a. ao*) passing above, the *posterior aorta* (*p. ao*) below the rectum. From the aortæ the blood passes into arteries (Fig. 96, *art.*,[1] *art*[2]) which ramify all over the body, finally forming an extensive network of vessels, many of which are devoid of proper walls and have therefore the nature of sinuses. The returning blood passes into a large longitudinal vein, the *vena cava*

(*v. c*), placed between the nephridia, whence it is taken to the kidneys themselves (*nph. v*), thence by *afferent branchial*

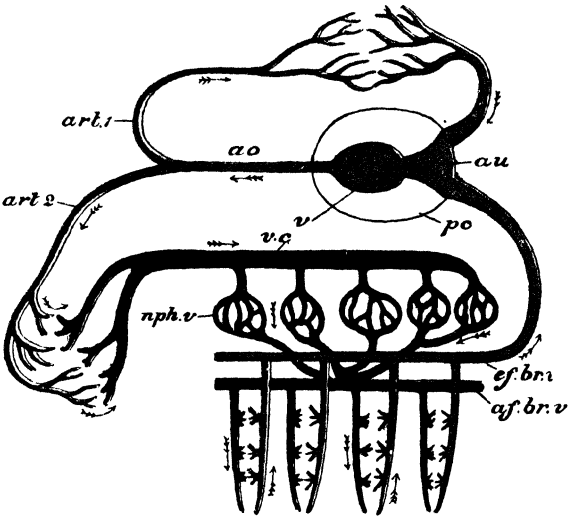

FIG. 96.—Diagram of the Circulatory System of Anodonta.
The blood received from the auricles (*au*) is pumped by the ventricle (*v*) into the aorta (*ao*) and thence passes to the mantle (*art.*[1]) and to the body generally (*art.*[2]).
The blood which has circulated through the mantle is returned directly to the auricle: that from the body generally is collected into the vena cava (*v. c*), passes by nephridial veins (*nph*) to the kidneys, thence by afferent branchial veins (*af. br. v*) to the gills, and is returned by efferent branchial veins (*ef. br. v*) to the auricles; *pc*, pericardium.
(From Parker and Haswell's *Zoology*.

veins (*af. br. v*) to the gills, and is finally returned by *efferent branchial veins* (*ef. br. v*) to the auricles. The mantle has a very extensive blood-supply, and probably acts as the chief

respiratory organ : its blood (*art*[1]) is returned directly to the auricles without passing through either the kidneys or the gills. The blood is colourless and contains leucocytes. There is no communication between the blood-system and the pericardium.

The nervous system is formed on a type quite different from anything we have yet met with. On each side of the gullet is a small *cerebro-pleural ganglion* (Fig. 94, *c. pl. gn*), united with its fellow of the opposite side by a nerve-cord, the *cerebral commissure*, passing above the gullet. Each cerebro-pleural ganglion also gives off a cord, the *cerebro-pedal connective*, which passes downwards and backwards to a *pedal ganglion* (*pd. gn*) situated at the junction of the visceral mass with the foot: the two pedal ganglia are so closely united as to form a single bilobed mass. From each cerebro-pleural ganglion there further proceeds a long *cerebro-visceral connective*, which passes directly backwards through the kidney, and ends in a *visceral ganglion* (*v. gn*) placed on the ventral side of the posterior adductor muscle. The visceral, like the pedal ganglia, are fused together. The cerebro-pleural ganglia supply the labial palps and the anterior part of the mantle; the pedal, the foot and its muscles; the visceral, the enteric canal, heart, gills, and posterior portion of the mantle.

It will be seen that the cerebral commissures and cerebro-pedal connectives, together with the cerebro-pleural and pedal ganglia, form a nerve-ring which surrounds the gullet: the cerebro-pleural ganglia may be looked upon as a supra-œsophageal nerve mass corresponding with the brain of Polygordius and the Crayfish, and the pedal ganglia as an infra-œsophageal mass representing the ventral nerve cord.

Sensory organs are poorly developed, as might be ex-

pected in an animal of such sedentary habits. In connection with each visceral ganglion is a patch of sensory epithelium forming the so-called olfactory organ or, better, *osphradium*, the function of which is apparently to test the purity of the water entering by the respiratory current. Close to the pedal ganglion is a minute *otocyst* or *statocyst*, the nerve of which is said to spring from the cerebro-pedal connective, being probably derived from the cerebral ganglion. Sensory cells, probably tactile, also occur round the edge of the mantle, and especially on the fimbriæ of the inhalant siphon.

The sexes are separate. The gonads (Figs. 93 and 94, *gon*) are large, paired, racemose bodies, occupying a considerable portion of the visceral mass amongst the coils of the intestine: the *spermary* is white, the ovary reddish. The gonad of each side has a short duct which opens (*g. ap*) on the surface of the visceral mass, just in front of the renal aperture.

In the breeding season the eggs, extruded from the genital aperture, pass into the supra-branchial chamber, and so to the cloaca. There, in all probability, they are impregnated by sperms introduced with the respiratory current. The oosperms are then passed into the cavities of the outer gills, which they distend enormously. Thus the outer gills act as brood-pouches, and in them the embryo develops into the peculiar larval form presently to be described.

The segmentation of the oosperm is remarkable for the fact that the cells of the polyplast are of two sizes, small cells composed entirely of protoplasm, and large cells loaded with yolk-granules. In the formation of the gastrula the large are invaginated into the small cells, but the enteron thus formed is very small and quite unimportant during early larval life, the young mussels being nourished, after

the manner of parasites, by a secretion from the gills of the parent.

The dorsal surface of the embryo is soon marked out by the appearance of a deep depression, the *shell-gland*, which secretes, in the first place, a single median shell. This is, however, soon replaced by a bivalved *larval shell* (Fig. 97, *s*), of triangular form, the ventral angles being produced into hooks (*sh*). The body at the same time becomes cleft from

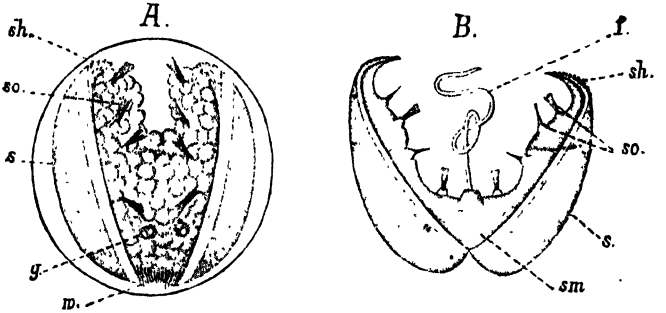

FIG. 97.—A, advanced embryo of Anodonta enclosed in the egg-membrane. B, free larva or glochidium.
f, byssus ; *g*, lateral pits ; *s*, shell ; *sh*, hooks ; *sm*, adductor muscle ; *so*, sensory hairs ; *w*, ciliated area.
(From Korschelt and Heider.)

below upwards (A), forming the right and left mantle-lobes. On the ventral surface, between the lobes of the mantle, is formed a glandular pouch, which secretes a bunch of silky threads, the *byssus* (*f*). The larva is now called a *glochidium*.

The glochidia, entangled together by means of their byssal threads, escape from the gills of the parent by the

exhalant siphon, and eventually attach themselves, by their hooked valves, to the body of a passing fish, such as a stickleback. Here they live for a time as external parasites, gradually undergoing metamorphosis; and finally drop from the host and assume the sedentary habits of the adult.

LESSON XXIX

THE DOGFISH

THE animals studied in the three previous Lessons have served to illustrate three widely different types of organization. The starfish is radially symmetrical, with an underlying bilateral symmetry, and no indication of metamerism: the crayfish is bilaterally symmetrical, metamerically segmented, and provided with numerous limbs, both trunk and limbs being covered with a hard, jointed armour or exoskeleton: the mussel is likewise bilaterally symmetrical, covered with a shell formed of paired pieces, and having no indication of metamerism, and no trace of limbs. We have now to consider, in the dogfish, an animal belonging to the great group of Vertebrata, in which the bilaterally symmetrical body is definitely divided into metameres, although there is no indication of the fact externally. There are only two pairs of limbs or paired appendages, and the main supporting structures are a complicated internal system of articulated hard parts, forming the *endoskeleton* or internal skeleton.

The commonest British dogfishes are the Rough Hound

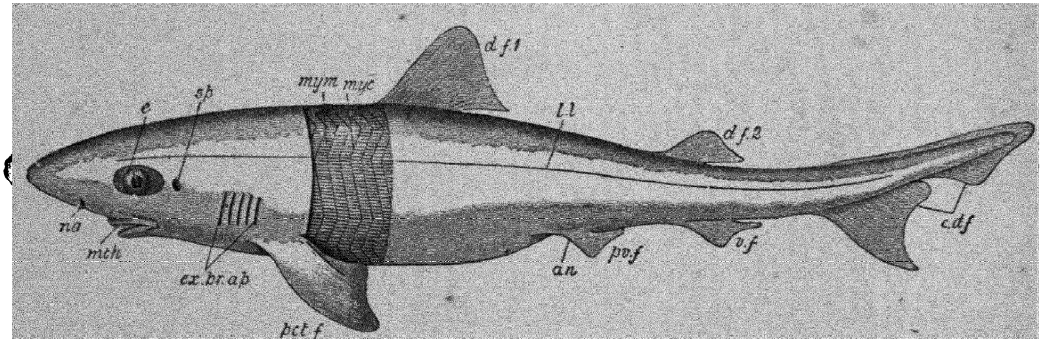

FIG. 98.—Side view of Dogfish (*Mustelus antarcticus*), with a strip of skin in the middle of the body removed to show the muscles.

an, position of anus; *cd. f*, caudal fin; *d. f.* 1, *d. f.* 2, dorsal fins: *e*, eye; *ext. br. ap*, external branchial apertures; *l. l*, lateral line; *mth*, mouth; *my. m*, myomeres; *my. c*, myocommas; *n. a*, nasal aperture; *pct. f*, pectoral fin; *pv. f*, pelvic fin; *sp*, spiracle; *v. f*, ventral fin.

(*Scyllium canicula*), the Lesser Spotted Dogfish (*S. catulus*), the Piked Dogfish (*Acanthias vulgaris*), and the Smooth Hound (*Mustelus vulgaris*). The following description, though referring mainly to *Scyllium*, will apply, in essential respects, to any of these.

The dogfish has a spindle-shaped body (Fig. 98), ending in front in a bluntly-pointed snout or cut-water, and behind tapering off into an upturned tail. On the ventral surface of the head is the large, transversely elongated *mouth* (*mth*), supported by a pair of jaws which work in a vertical, and not, like those of the crayfish, in a transverse plane, and are, in fact, portions of the skull, having nothing to do with limbs. They are covered with teeth which vary in form in the different species. In front of the mouth, on the ventral surface of the snout, are the paired *nostrils* (*na*), each leading into a cup-like *nasal sac*. The *eyes* (*e*) are also two in number and are placed one on each side of the head, above the mouth. Behind the mouth are five slit-like apertures (*ex. br. ap*), arranged in a longitudinal series: these are the *gill-clefts* or *external branchial apertures*. Just behind the eye is a small aperture, the *spiracle* (*sp*): like the gill-clefts, it communicates with the pharynx, and it is found by development to be actually the functionless first gill-cleft.

On the ventral surface of the body, about half-way between its two ends, is the *anus* or *cloacal aperture* (*an*), and on either side of it a small hole, the abdominal pore, opening into the cœlome. From the end of the snout to the last gill-cleft is considered as the *head* of the fish; from the last gill-cleft to the anus as the *trunk*; and the rest as the *tail*.

A longitudinal streak (*l. l*) on each side of the body, connected in front with a series of branching lines on the head and continued backwards to the tail, is known as the *lateral*

line. The whole apparatus, together with other canals in the head, is really a system of tubes sunk in the skin, and constitutes an important, but imperfectly understood, sensory organ.

Springing from the body are a number of flattened folds, called the *fins*, divisible into *median* and *paired*. The median folds are two *dorsal fins* (*d. f.* 1, *d. f.* 2) along the middle line of the back, a *caudal fin* (*cd. f*) lying mostly along the ventral edge of the upturned tail, and a *ventral fin* (*v. f*) behind the anus. The paired folds are the *pectoral fins* (*pct. f*), situated one on each side of the trunk just behind the last gill-cleft, and the *pelvic fins*, one on each side of the anus. The pectoral and pelvic fins are the paired appendages or limbs of the dogfish: as in other Vertebrates there are only two pairs, the pectorals corresponding with the fore-limbs, the pelvics with the hind limbs of the higher forms.

The fish swims by vigorous strokes of the tail: the pectoral fins are used chiefly for steering, and the dorsal and ventral fins serve, like the keel of a boat, to maintain equilibrium.

The skin or external layer of the body-wall consists, as usual, of two layers, an outer layer of deric epithelium (Fig. 99, *Der. Epthm*) differing from that of previous types in being formed of several layers of cells, and an inner layer of connective tissue, the dermis. In the dermis are innumerable close-set calcareous bodies (Fig. 99, *Derm. Sp*), each consisting of a little irregular plate of bone produced into a short enamelled spine, which projects through the epidermis and gives a rough, sand-paper-like character to the skin. These *placoid scales* or *dermal teeth* together constitute the exoskeleton of the dogfish: it is a discontinuous dermal exoskeleton like that of the starfish.

Beneath the dermis is the muscular layer in which we

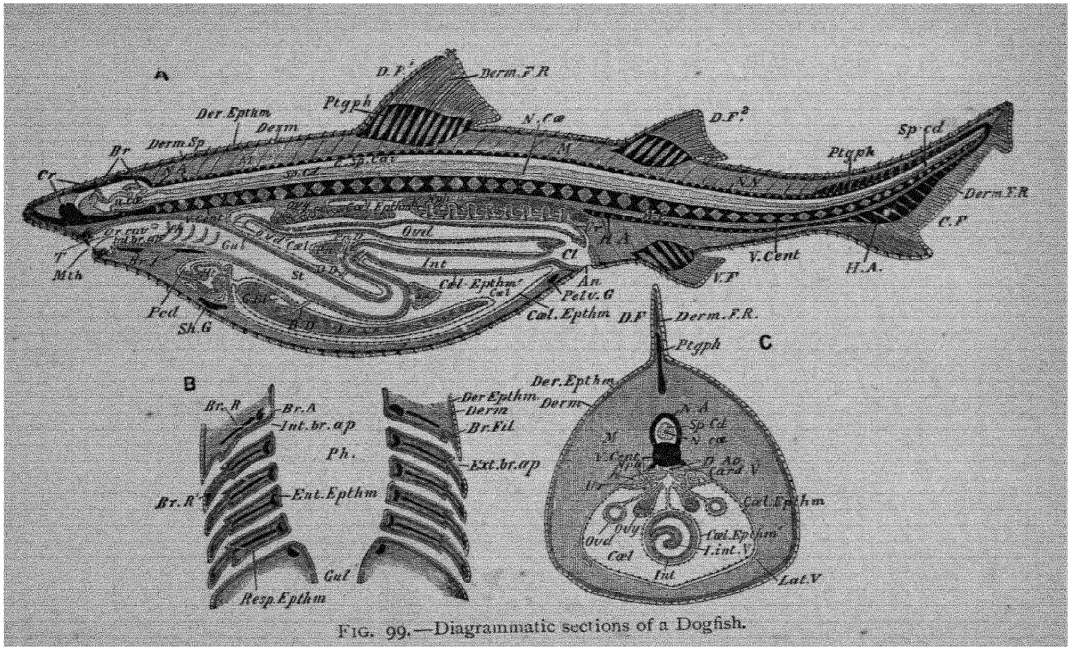

FIG. 99.—Diagrammatic sections of a Dogfish.

A, longitudinal vertical section.

B. horizontal section through the pharynx and gills.

C, transverse section through the trunk.

The ectoderm is dotted, the nervous system finely dotted, the endoderm radially striated, the mesoderm evenly shaded, the cœlomic epithelium represented by a beaded line, and all skeletal structures black.

The body gives origin to the dorsal (*D. F*^{1}, *D. F*^{2}), ventral (*V. F*), and caudal (*C. F*) fins; the paired fins are not shown.

The body-wall consists of deric epithelium (*Der. Epthm*), dermis (*Derm*), and muscle (*M*): the latter is metamerically segmented and is very thick, especially dorsally, where it forms half the total vertical height (C).

The exoskeleton consists of calcified dermal spines (*Derm. Sp*) in the dermis, and of dermal fin-rays (*Derm. F. R*) in the fins.

The endoskeleton consists of a row of vertebral centra (*V. Cent*) below the spinal cord (*Sp. Cd*), giving rise to neural arches (*N. A*), which enclose the cord, and in the caudal regions to hæmal arches (*H. A*): a cranium (*Cr*) enclosing the brain (*Br*): upper and lower jaws: branchial arches (*Br. A*) and rays (*Br. R*, *Br. R'*), shown only in B, supporting the gills: shoulder (*Sh. G*) and pelvic (*Pelv. G*) girdles: and pterygiophores (*Ptgph*) supporting the fins.

The mouth (*Mth*) leads into the oral cavity (*Or. cav*), from which the pharynx (*Ph*) and gullet (*Gul*) lead to the stomach (*St*): this is connected with a short intestine (*Int*) opening into a cloaca (*Cl*) which communicates with the exterior by the vent (*An*). The oral cavity and cloaca are the only parts of the canal lined by ectoderm.

Connected with the enteric canal are the liver (*Lr*) with the gall-bladder (*G. Bl*) and bile-duct (*B. D*), the pancreas (*Pn*), and the spleen (*Spl*). The mouth is bounded above and below by teeth (*T*).

The respiratory organs consist of pouches (shown in B) communicating with the pharynx by internal (*Int. br. ap*) and with the exterior by external (*Ext. br. ap*) branchial apertures, and lined by mucous membrane raised into branchial filaments (*Br. Fil*).

The heart (*Ht*) is ventral and anterior, and is situated in a special compartment of the cœlome (*Pcd*). Six of the most important blood-vessels, the dorsal vessel (dorsal aorta, *D. Ao*), the cardinal veins (*Card. V*), the lateral vessels (lateral veins, *Lat. V*), and the ventral vessel (intra-intestinal vein, *I. int. V*) are shown in C.

The whole cœlome is lined by epithelium, showing parietal (*Cœl. Epthm*) and visceral (*Cœl. Epthm'*) layers.

The ovaries (*Ovy*) are connected with the dorsal body-wall: the oviducts (*Ovd*) open anteriorly into the cœlome (*ovd'*) and posteriorly into the cloaca.

The kidneys (*K*) are made up of nephridia (*Nph*) and open by ureters (*Ur*) into the cloaca.

The nervous system is lodged in the cerebro-spinal cavity (*C. Sp. Cav*) hollowed out in the dorsal body-wall: it consists of brain (*Br*) and spinal cord (*Sp. Cd*), and contains a continuous cavity, the neurocœle (*n. cœ*).

meet, for the first time in our present subject, with distinct metameric segmentation. The muscles are divided into segments or *myomeres* (Fig. 98, *mym*) following one another from before backwards, and having a zigzag disposition. The fibres composing them are longitudinal, and are inserted at either end into fibrous partitions or *myocommas* (*myc*), which separate the myomeres from one another. The muscular layer is of great thickness, especially its dorsal portion (Fig. 99, c). The fibres of all the body muscles are of the striped kind.

There is a large *cœlome* (Fig. 99, *Cœl*), remarkable for being confined to the trunk, both head and tail being, in the adult, accœlomate. The cavity is divisible into two parts: a large *abdominal cavity*, containing most of the viscera, and a small anterior and ventral compartment, the *pericardial cavity* (*Pcd*), containing the heart. Both are lined by cœlomic epithelium (*Cœl. Epthm*), underlain by a layer of connective tissue, a strong lining membrane being thus produced, called *peritoneum* in the abdominal, *pericardium* in the pericardial cavity.

Another very characteristic feature is that the dorsal body-wall is tunnelled, from end to end, by a median longitudinal *neural cavity*, in which the central nervous system is contained. The greater part of the cavity is narrow and cylindrical, and contains the spinal cord: its anterior or cerebral portion is dilated, and contains the brain.

Imbedded in the body-wall and extending into the fins are the various parts of the *endoskeleton*. This characteristic supporting framework is formed of a tough elastic tissue called *cartilage* or gristle, more or less impregnated with lime salts, so as to have, in part, the appearance of bone. As, however, the hard parts of the dogfish's skeleton have a different microscopic structure from the bones of the higher vertebrates, they are best described as *calcified cartilage*.

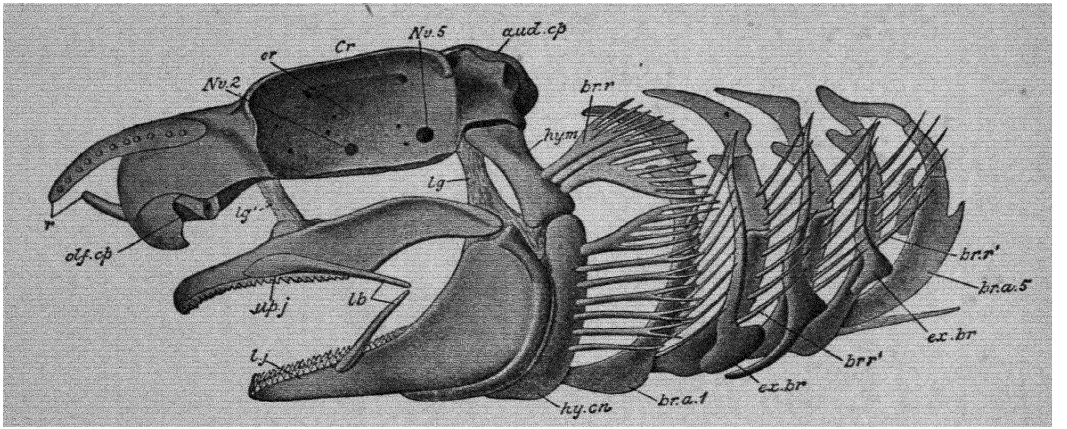

FIG. 100.—Side view of skull of *Scyllium canicula*.

The cranium (*Cr*) shows the projecting auditory capsule (*aud. cp*), the hollow orbit (*or*), the olfactory capsule (*olf. cp*) and the cartilages of the rostrum or beak (*r*). In the orbit are seen apertures for the optic (*Nv.* 2) and trigeminal (*Nv.* 5) nerves.

Articulated with the auditory capsule is the hyomandibular (*hy. m*), helping to support the upper (*up. j*) and lower (*l. j*) jaws, and giving attachment below to the hyoid cornu (*hy. cn*); the upper jaw is also attached to the cranium by two ligaments (*lg*, *lg'*), and small labial cartilages (*lb*) are connected with them.

Following upon the hyoid cornu (*hy. cn*) come the five branchial arches (*br. a.* 1–5): from these, as well as from the hyomandibular and hyoid cornu are given off branchial rays (*br. r*, *br. r'*), which are connected externally with extra-branchial cartilages (*ex. br*).

(After W. K. Parker.)

The entire skeleton consists of separate pieces of cartilage, calcified or not, and connected with one another by sheets or bands of connective tissue called *ligaments*: it is divisible into the following parts:—

A. The *skull* or skeleton of the head, consisting of—
   1. The *cranium* or brain-case, enclosing the brain and the chief sense-organs.
   2. The *upper* and *lower jaws*.
   3. The *visceral arches*, a series of cartilaginous hoops supporting the gills.

B. The *vertebral column* or "backbone," a jointed axis extending from the cranium to the end of the tail, and enclosing the spinal cord.

C. The skeleton of the *median fins*.

D. The skeleton of the paired fins, consisting of—
   1. The *shoulder-girdle* or *pectoral arch*, to which are attached
   2. The *pectoral fins*.
   3. The *hip-girdle* or *pelvic arch*, to which are attached
   4. The *pelvic fins*.

The cranium (Fig. 100, *Cr*) is an irregular cartilaginous box containing a spacious cavity for the brain, and produced into two pairs of outstanding projections: a posterior pair, called the *auditory capsules* (*aud. cp*), for the lodgment of the organs of hearing, and an anterior pair, the *olfactory capsules* (*olf. cp*), for the organs of smell. Between the olfactory and auditory capsules, on each side, the cranium is hollowed out into an *orbit* (*or*) for the reception of the eye. In front the cranium is produced into three cartilaginous rods (*r*), which support the snout. On its posterior

face is a large aperture, the *foramen magnum*, through which the brain joins the spinal cord, and on each side of the foramen is an oval elevation or *condyle* for articulation with the first vertebra.

In the human and other higher vertebrate skulls the upper jaw is firmly united to the cranium, and the lower alone is free. But in the dogfish both jaws (*up. j*, *l. j*) are connected with the cranium by ligament (*lg*, *lg'*) only, and each consists of strong paired (right and left) moieties, united with one another by fibrous tissue. The posterior end of the upper jaw presents a rounded surface, on which fits a corresponding concavity on the lower jaw, so that a free articulation is produced, the lower jaw working up and down in the vertical plane, not from side to side like the jaws of the crayfish.

The visceral arches consist of six pairs of cartilaginous half-hoops, lying in the walls of the pharynx (Fig. 99, B, *Br. A*), and united with one another below so as to form a basket-like apparatus supporting the gills. The first of these arches is distinguished as the *hyoid*, and is situated immediately behind the jaws. It consists of two parts, a strong, rod-like *hyomandibular* (Fig. 100, *hy. m*), which articulates above with the auditory capsule, and is connected below by fibrous tissue with the jaws, thus helping to suspend them to the cranium: and a *hyoid cornu*, which curves forwards inside the lower jaw, and is connected with its fellow of the opposite side by a median plate which supports the tongue.

The remaining five arches (*br. a.* 1—*br. a.* 5) are called the *branchial arches*. Each is formed of several separate pieces, movably united by fibrous tissue so as to render possible the distension of the throat during swallowing. Both they and the hyoid give attachment to delicate cartilaginous *branchial rays* (*br. r*, *br. r'*: Fig. 99, *Br. R*) which support the gills.

The vertebral column has the general character of a jointed tube surrounding the spinal portion of the neural canal. Lying beneath this cavity, *i.e.*, between it and the cœlome, is a longitudinal row of biconcave discs, the *ver-*

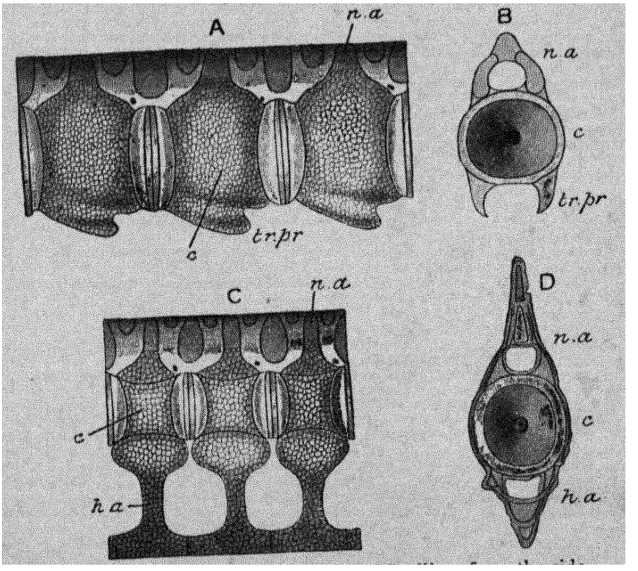

FIG. 101.—A, Three trunk vertebræ of Scyllium from the side.
B, a single trunk vertebra viewed from one end.
C, three caudal vertebræ from the side.
D, a single caudal vertebra from one end.
c, centrum ; *h. a*, hæmal arch ; *n. a*, neural arch ; *tr. pr.* transverse process.
(After Hasse.)

tebral centra (Fig. 101, *c* ; Fig. 99, *V. Cent*) : they are formed of cartilage, but have their anterior and posterior faces strongly calcified. The biconcave intervals between them (Fig. 99, A) are filled with a gelatinous matter or *inter-*

vertebral substance. The centra are united by ligament, so that the whole chain of discs is very flexible. Connected with the dorsal aspect of the series of centra is a cartilaginous tunnel, arching over the spinal cord: it is divided into segments, corresponding with, but usually twice as numerous as the centra, and called the *neural arches* (Fig. 101, *n. a;* Fig. 99, *N. A*).

In the anterior part of the vertebral column the centra give off paired outstanding processes (Fig. 101, A and B, *tr. pr*) called *transverse processes*, to the end of each of which is articulated a short cartilaginous rod, the *rib*. Further back the transverse processes are directed downwards, instead of outwards, and in the whole caudal or tail region they unite below, forming *hæmal arches* (Fig. 101, C and D, *h. a;* Fig. 99, A, *H. A*), which together constitute a kind of inverted tunnel in which lie the artery and vein of the tail. In the region of the caudal fin the hæmal arches are produced into strong median *hæmal spines* (Fig. 99, A, *H. A* to the right), which act as supports to the fin. A centrum, together with the corresponding neural arch and transverse processes or hæmal arch, forms a *vertebra* or single segment of the vertebral column.

It should be noticed that in the vertebral column we have another instance of the metameric segmentation of the vertebrate body. The vertebræ do not, however, correspond with the myomeres, but alternate with them. The myocommas are attached to the middle of the vertebræ, so that each myomere acts upon two vertebræ and thus produces the lateral flexion of the backbone.

In the embryo, before the development of the vertebral column, an unsegmented gelatinous rod, the *notochord*, lies beneath the neural cavity in the position occupied in the adult by the line of centra, by the development of which it

is largely replaced. Much of it, however, remains as the gelatinous intervertebral substance. The notochord is one of the most characteristic organs of the Vertebrata.

The skeleton of the median fins consists of a series of parallel cartilaginous rods, the *fin-rays* or *pterygiophores*

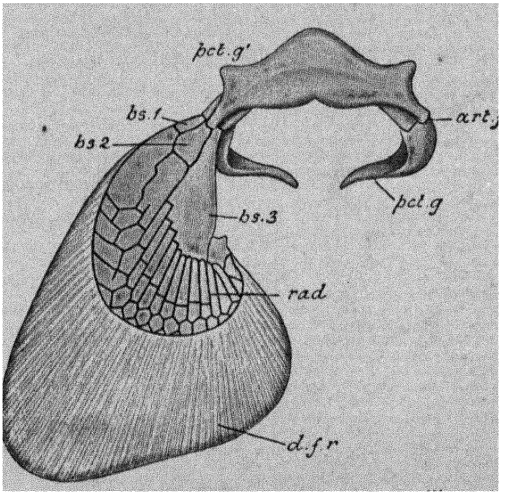

FIG. 102.—Ventral view of pectoral arch of Scyllium with right pectoral fin.

The pectoral arch is divisible into dorsal (*pct. g*) and ventral (*pct. g'*) portions separated by the articular facets (*art. f*) for the fin.

The pectoral fin is formed of three basal cartilages (*bs.* 1-3) and numerous radials (*rad*); its free edge is supported by dermal rays (*d. f. r*).

(Modified from Marshall and Hurst.)

(Fig. 99, *Pygph*), the proximal ends of which are more or less fused together to form basal cartilages or *basalia*. The free edges of the fins are supported by a double series of delicate horn-like fibres, the *dermal fin-rays* (*Derm. F. R*).

The shoulder-girdle (Fig. 102) is a strong, inverted arch of

calcified cartilage, situated just behind the last branchial arch (Fig. 99, A, *Sh. G*). On each side of its outer surface it presents three elevations or *articular facets* (Fig. 102, *art. f*) for the pectoral fin; the presence of these allows of the division of each side of the arch into a narrow, pointed dorsal portion (*pct. g*), and a broader ventral portion (*pct. g'*) united in the middle line with its fellow of the opposite side. The pectoral fin is formed of pterygiophores (*rad*), fused proximally to form basals (*Bs.* 1.—3), which are three in number, and very large and strong.

The pelvic girdle is a transverse bar of cartilage situated just in front of the vent (Fig. 99, A, *Pelv. G*), and presenting on its posterior edge facets for the pelvic fin. The latter has the same general structure as the other fins, but has a single very large basal cartilage, and its first or anterior radial is also much enlarged. The free edges of both pectoral and pelvic fins are supported by horn-like dermal rays (Fig. 102, *d.f.r*).

It will be noticed that while the skeleton of the crayfish is a series of articulated tubes with the muscles inside them, that of the dogfish is a series of articulated rods with the muscles outside. The joints, formed by two rods applied at their ends and bound together by ligament, are not confined to movement in one plane, like the hinge-joints of the crayfish, but are capable of more or less rotatory movement.

The mouth, as we have seen, is a transverse aperture bounded by the upper and lower jaws. In the mucous membrane covering the jaws are imbedded large numbers of *teeth*, (Fig. 99, *T*) bony conical bodies, with enamelled tips, arranged in transverse rows. They are to be looked upon as special developments of the placoid scales or dermal teeth, enlarged for the purpose of seizing prey.

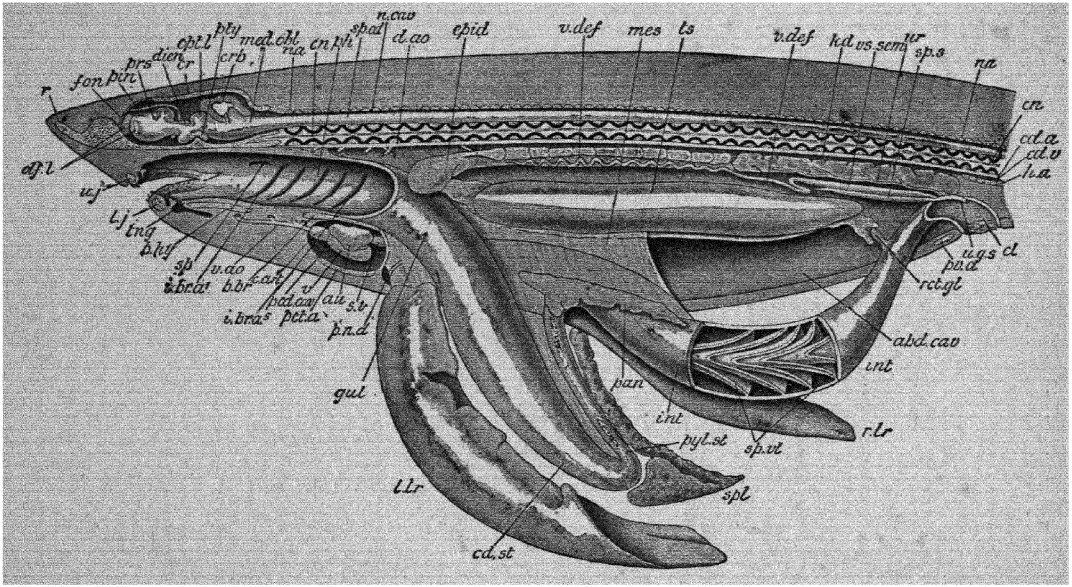

FIG. 103.—Dissection of *Scyllium canicula* from the left side. The left side of the body-wall is cut away to the median plane so as to expose the abdominal (*abd. cav*), pericardial (*pcd. cav*) and neural (*n. cav*) cavities in their whole length.

In the skeleton the cartilaginous parts are dotted, the bony ends of the vertebræ black. *cn*, centra; *n. a*, neural arches; *h. a*, hæmal arches; *cr*, cranium; *r*, rostrum; *u. j*, upper jaw; *l. j*, lower jaw; *b. hy*, basi-hyal, supporting tongue (*tng*); *b. br*, basi-branchial; *pct. a*, pectoral arch; *pv. a*, pelvic arch. The front part of the cranium is roofed by a membranous fontanelle (*fon*).

The enteric canal with the liver (*l. lr*, *r. lr*), &c., has been displaced downwards, and the oral cavity and pharynx (*ph*), part of the intestine (*int*), and the cloaca (*cl*) have been opened. *sp*, spiracle; *i. br. a*^{1}-*i. br. a*^{5}, internal branchial apertures; *cd. st*, cardiac, and *pyl. st*, pyloric portions of stomach; *sp. vl*, spiral valve of intestine (*int*); *l. lr*, left, and *r. lr*, right lobe of liver; *pan*, pancreas; *spl*, spleen; *rct. gl*, rectal gland; *mes*, mesentery.

The heart consists of sinus venosus (*s. v*), auricle (*au*), ventricle (*v*), and conus arteriosus (*c. art*): the latter gives off the ventral aorta (*v. ao*) from which are seen to arise the afferent branchial arteries of the right side. The dorsal aorta (*d. ao*) receives anteriorly the efferent branchial arteries, and posteriorly becomes the caudal artery (*cd. a*), lying above the caudal vein (*cd. v*).

The spinal cord (*sp. cd*) passes in front into the brain, which consists of medulla oblongata (*med. obl*), cerebellum (*crb*), optic lobes (*opt. l*), diencephalon (*dien*), proscephalon (*prs*), and olfactory lobes (*olf. l*). To the diencephalon are attached the pineal (*pin*) and pituitary (*pty*) bodies.

The left kidney (*kd*) opens by the ureter (*ur*) into the urinogenital sinus (*u. g. s*) which discharges into the cloaca. The left spermary (*ts*) is connected with the epididymis (*epid*) from which the vas deferens (*v. def*) passes backwards, dilates into the vesicula seminalis (*vs. sem*) and opens into the urinogenital sinus, with which is also connected the sperm-sac (*sp. s*). Attached to the fold of peritoneum supporting the liver is a small tube (*p. n. d*) representing the oviduct of the female.

The mouth (Figs. 99, *Mth* and 103) leads into an *oral cavity* (*Or. cav*), which passes insensibly into the throat or *pharynx* (*ph*), a division of the enteric canal distinguished by having its walls perforated by five pairs of slits, the *internal branchial apertures* (*i. br. a* 1–5) as well as by the inner opening of the spiracle (*sp*). The pharynx is continued by a short gullet (*gul*) into a capacious U-shaped *stomach* consisting of a wide cardiac division (*cd. st*) and a narrow pyloric (*pyl. st*) division. The pyloric division communicates by a narrow valvular aperture with the *intestine* (*int*), a wide, nearly straight tube having its lining membrane produced into a spiral fold, the *spiral valve* (*sp. vl*), which practically

converts the intestine into a very long, closely-coiled tube, and greatly increases the absorbent surface. Finally the intestine opens into a large chamber, the *cloaca* (*cl*), which communicates with the exterior by the vent.

From the gullet backwards the enteric canal is contained in the abdominal division of the cœlome, to the dorsal wall of which it is suspended by a median mesentery (Fig. 99, C, and Fig. 103, *mes*). The greater part of the canal is developed from the enteron of the embryo, and is consequently lined by endoderm; only the oral cavity is formed from the stomodæum, and the cloaca from the proctodæum (Fig. 99, A). Outside the enteric epithelium are connective and muscular layers, the latter formed of unstriped fibres: it is generally characteristic of Vertebrates that the voluntary muscles are striped, the involuntary unstriped.

The digestive glands are characteristic. The largest is an immense *liver* (Fig. 99, *Lr*) divided into two lobes (Fig. 103, *l. lr*, *r. lr*) and situated below the stomach along the whole length of the abdomen, to the wall of which it is attached by a fold of peritoneum. It discharges its secretion, the *bile*, into the commencement of the intestine by a tube, the *bile-duct* (Fig. 99, *B. D*), which gives off a blind offshoot terminating in a large sac, the *gall-bladder* (*G. Bl*); this serves as a reservoir for the bile, the chief function of which is to act upon the fatty portions of the food. But besides secreting this special digestive juice, the liver-cells produce a substance called *glycogen* or animal starch, which is passed directly into the blood in the form of sugar.

Another gland, of considerably smaller size, is the pancreas (Fig. 99, *Pn* Fig. 103, *pan*); it lies against the anterior end of the intestine, into which it opens by the *pancreatic duct*. It secretes *pancreatic juice*, which has an action upon all the principal classes of food, converting

proteids into peptones, starch into sugar, and breaking up fats. Opening into the cloaca is a small finger-like *rectal gland* (*rct. gl*), the function of which is uncertain.

In addition to these glands the inner surface of the stomach and intestine is dotted all over with microscopic apertures, leading into minute tubular glands sunk in the mucous membrane. These are the *gastric* and *intestinal glands:* the former secrete *gastric juice*, which digests proteids; the latter *intestinal juice*, which probably acts upon all classes of food. Thus as compared with the animals previously studied, the dogfish, in common with other Vertebrates, shows an extraordinary differentiation of digestive glands and fluids.

There is another characteristic vertebrate organ in close connection with the enteric canal and called the *spleen* (*spl*). It is an irregular dark-red, gland-like body, of considerable size, attached by peritoneum to the stomach. It has no duct, and its chief function is probably the manufacture of leucocytes and the disposal of worn-out red blood corpuscles. Other *ductless glands* are the *thyroid* in the throat; the *thymus* in connection with the dorsal ends of the branchial arches; and the *supra-* and *inter-renal bodies* in relation with the kidneys.

The respiratory organs or *gills* consist of five pairs of pouches, each opening by one of the internal branchial apertures (Figs. 99, A and B, *Int. br. ap* and 103) into the pharynx, and by one of the external branchial apertures (*Ext. br. ap*) on the exterior. The walls of the pouches are supported by the visceral arches (*Br. A*) and branchial rays (*Br. R*, *Br. R'*), and are lined with mucous membrane raised into horizontal ridges, the *branchial filaments* (*Br. Fil*), which are abundantly supplied with blood-vessels, and are the actual organs of respiration. As the fish swims, water

enters the mouth and passes by the internal clefts into the branchial pouches, and thence outwards by the external clefts, a constant supply of oxygen being thus ensured. The gill-pouches are developed as offshoots of the pharynx, and the respiratory epithelium is therefore endodermal, not ectodermal, as in the starfish, crayfish, and mussel.

The organs of circulation attain a degree of specialisation not met with in any of our former types. The heart is situated in the pericardial cavity or anterior compartment of the cœlome, and is a large muscular organ composed of four chambers. Posteriorly is a small, thin-walled *sinus venosus* (Figs. 103 and 104, *s. v*), opening in front into a capacious thin-walled *auricle* (*au*); this communicates with a very thick-walled *ventricle* (*v*), from which is given off in front a tubular chamber, also with thick muscular walls, the *conus arteriosus* (*c. art*). There are valves between the sinus and the auricle, and between the auricle and ventricle, and the conus contains three longitudinal rows of valves: all the valves are arranged so as to allow of free passage of blood from sinus to auricle, auricle to ventricle, and ventricle to conus, but to prevent any flow in the opposite direction. The heart, alone among the involuntary muscles, is formed of striped fibres.

The conus gives off in front a single blood-vessel (*v. ao*), having thick elastic walls composed of connective and elastic tissue and unstriped muscle. This vessel, the *ventral aorta*, passes forwards beneath the gills, and gives off on each side paired lateral branches, the *afferent branchial arteries* (*a. br. a*). Each afferent artery passes to the corresponding gill, and there branches out into smaller and smaller arteries, which finally become microscopic, and open into a network of delicate tubes called *capillaries*, with which the connective tissue of the branchial filaments is permeated. The

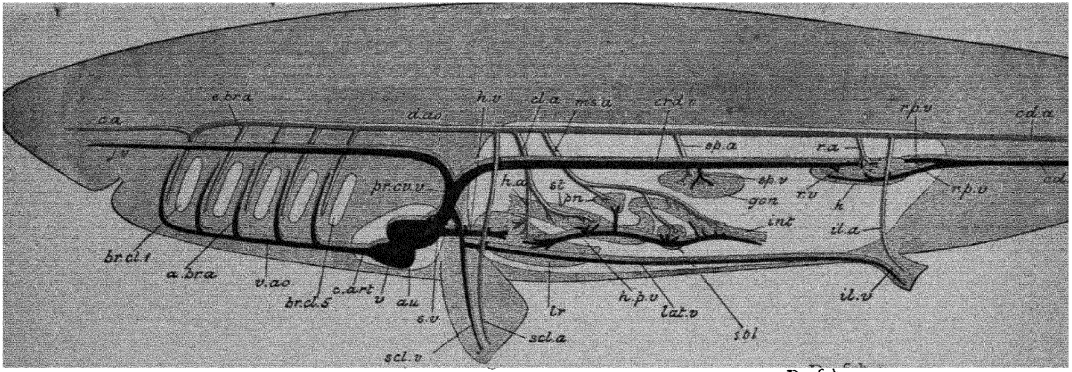

FIG. 104.—Semi-diagrammatic side-view of the vascular system of a Dogfish.

The heart consists of sinus venosus (*s. v*), auricle (*au*), ventricle (*v*), and conus arteriosus (*c. art*), with valves opening forwards.

From the conus goes off the ventral aorta (*v. ao*), which gives off afferent branchial arteries (*a. br. a*) to the gills; after aëration the blood is taken by efferent branchial arteries (*e. br. a*) to the dorsal aorta (*d. ao*).

The head is supplied with pure blood by the carotid arteries (*c. a*), the pectoral fins by the subclavians (*scl. a*), the stomach (*st*) and liver (*lr*) by the cœliac (*cl. a*), the intestine (*int*), pancreas (*pn*), and spleen (*spl*) by the mesenteric (*ms. a*), the gonads by the spermatics (*sp. a*), the kidneys by the renals (*r. a*), the pelvic fins by the iliacs (*il. a*), and the tail by the caudal (*cd. a*).

The blood is returned from the head by the jugular veins (*j. v*), from the tail by the caudal (*cd. v*) which divides into the renal portal veins (*r. p. v*) going to the kidneys: thence the blood is taken by the renal veins (*r. v*) into the cardinals (*crd. v*), which also receive the spermatic veins (*sp. v*) from the gonads and join with the jugulars to form the precavals (*pr. cv. v*) opening into the sinus venosus.

The blood from the stomach, intestine, spleen, and pancreas is taken by the hepatic portal vein (*h. p. v*) to the liver and thence by the hepatic veins (*h. v*) to the sinus venosus.

The blood from the pectoral fin is taken by the subclavian vein (*scl. v*), that from the pelvic fin by the iliac vein (*il. v*) and passed into the lateral vein (*lat. v*), which discharges into the sinus venosus.

(From Parker and Haswell's *Zoology*.)

capillaries, unlike the arteries, have no muscle or connective tissue in their walls, which are formed of a single layer of epithelial cells. The blood in these *respiratory capillaries* is therefore brought into close relation with the surrounding water, and as the blood flows through them it exchanges its carbon dioxide for oxygen.

From the respiratory capillaries the blood is collected into minute arteries, which join into larger and larger trunks, and finally unite into *efferent branchial arteries* (*ebr. a*—two to each gill—by which the purified blood is carried from the gills. The efferent arteries of the right and left sides unite in a median longitudinal artery, the *dorsal aorta* (*d. ao*), which passes backwards, immediately beneath the vertebral column, to the end of the tail.

From the efferent branchial arteries and the dorsal aorta are given off numerous arteries supplying the whole of the body with blood. The most important of these are two pairs of *carotid arteries* (*c. a*) to the head, a pair of *subclavians* (*scl. a*) to the pectoral fins, unpaired *cœliac* (*cl. a*) and *mesenteric arteries* (*ms. a*) to the enteric canal, liver, pancreas, and spleen, numerous paired *renals* (*r. a*) to the kidneys, *spermatics* (*sp. a*) to the gonads, and a pair of *iliacs* (*il. a*) to the pelvic fins. The posterior part of the dorsal aorta, supplying the tail, is contained in the hæmal canal of the caudal vertebræ, and is known as the *caudal artery* (*cd. a*).

All these arteries branch and branch again in the various parts to which they are distributed, their ultimate ramifications opening, as in the case of the gills, into a capillary network with which every tissue, except the cartilages and the epithelia, is permeated. In traversing these *systemic capillaries* the blood parts with its oxygen and various nutrient matters to the tissues, and receives from them carbon dioxide and other waste matters.

From the systemic as from the respiratory capillaries the blood is collected into vessels which join into larger and larger efferent trunks. But these trunks are not thick-walled elastic arteries, but thin-walled, non-elastic, collapsible tubes, having valves at intervals, called *veins*. As a general rule every part of the body has a vein running alongside its artery, the blood in the artery flowing to the part in question, that of the vein away from it.

The blood from the head is brought back by a pair of *jugular veins* (*j. v*): each of these enters a large *precaval vein* (*pr. cv. v*), which passes vertically downwards and enters the sinus venosus. The blood from the tail is returned by a *caudal vein* (*cd. v*) lying immediately beneath the caudal artery in the hæmal canal: this vessel enters the cœlome and then divides into right and left branches, the *renal portal veins* (*r. p. v*), which pass to the kidneys and join with the capillaries of these organs, the impure blood brought from the tail mingling with the pure blood of the renal arteries (*r. a*). From the kidneys the blood is returned into a pair of immense *cardinal veins* (*crd. v*), which pass forwards, receiving veins from the reproductive organs (*sp. v*), muscles, &c., and finally join each with the corresponding jugular to form the precaval vein.

From the stomach, intestine, spleen, and pancreas the blood is collected by numerous veins, which all join to form a large *hepatic portal vein* (*h. p. v*). This behaves in the same way as the renal portal: instead of joining a larger vein on its way to the heart, it passes to the liver and breaks up to connect with the capillaries of that organ, its blood, deprived of oxygen but loaded with nutrient matters from the enteric canal, mingling with the oxygenated blood brought to the liver by a branch of the cœliac artery. After circulating through the capillaries of the liver the blood

is taken by a pair of *hepatic veins* (*h. v*) to the sinus venosus.

The *iliac veins* (*il. v*) from the pelvic fins pour their blood into the *lateral veins* (*lat. v*), paired trunks running forwards in the side walls of the body to the sinus venosus, and receiving at their anterior ends the *subclavian veins* (*scl. v*) from the pectoral fins.

Some of the veins, especially the cardinals and spermatics, are dilated into spacious cavities called *sinuses*. These are, however, of a totally different nature from the sinuses of the crayfish, which are mere spaces among the tissues devoid of proper walls. In the dogfish, as in Vertebrata generally, the blood is confined, throughout its course, to definite vessels, the heart, arteries, capillaries, and veins invariably forming a closed system of communicating tubes.

The general course of the circulation will be seen to agree with that already described in the crayfish and mussel: *i.e.*, the blood is driven by the contractions of the heart through the arteries to the various tissues of the body, whence it is returned to the heart by the veins or sinuses (compare Figs. 88, 96, and 104A). But whereas in both crayfish and mussel the respiratory organs are interposed in the returning current, both their afferent and efferent vessels being veins, in the dogfish they are interposed in the outgoing current, their afferent and efferent vessels being arteries. An artery, it must be remembered, is a vessel taking blood from the heart to the tissues of the body, and having thick walls to resist the strain of the heart's pulsation; a vein is a thin-walled vessel bringing back the blood from the tissues to the heart.

Moreover, the circulation in the dogfish is complicated by the presence of the two portal systems, renal and hepatic. In both of these we have a vein, renal portal or hepatic

portal, which, instead of joining with larger and larger veins, and so returning its blood directly to the heart, breaks up, after the manner of an artery, in the kidney or liver, the blood finding its way into the ordinary venous channels after having traversed the capillaries of the gland in question.

Thus an ordinary artery arises from the heart or from an

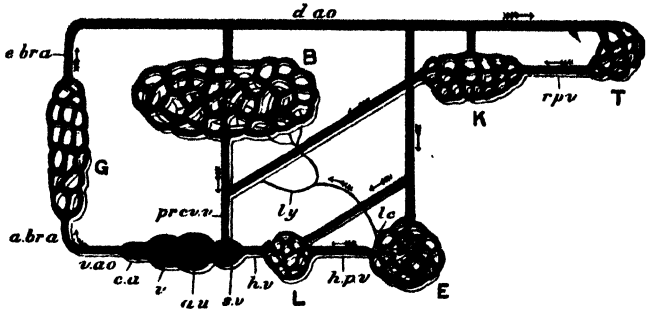

FIG. 104A.—Diagram illustrating the course of the circulation in the Dogfish.

Vessels containing oxygenated blood, red; non-oxygenated, blue. *B*, capillaries of the body generally; *E*, of the enteric canal; *G*, of the gills; *K*, of the kidneys; *L*, of the liver; *T*, of the tail.

a, br. a, afferent branchial arteries, *au*, auricle; *c. a*, conus arteriosus; *d. ao*, dorsal aorta; *e. br. a*, efferent branchial arteries; *h. p. v*, hepatic portal vein; *h. v*, hepatic vein; *lc*, lacteals; *ly*, lymphatics; *pr. cv. v*, precaval vein; *r. p. v*, renal portal vein; *s. v*, sinus venosus; *v*, ventricle; *v. ao*, ventral aorta.

The arrows show the direction of the current.

(From Parker and Haswell's *Zoology*.)

artery of higher order and ends in capillaries; an ordinary vein arises from a capillary network and ends in a vein of higher order or in the heart. But the hepatic and renal portal veins end in capillaries after the manner of arteries, and the efferent branchial arteries begin in capillaries after the manner of veins.

With regard to the general morphology of the blood-system, the dorsal aorta with the caudal artery may be considered as a dorsal vessel (compare Polygordius, p. 279, and Crayfish, p. 340), the caudal vein, hepatic portal vein, heart, and ventral aorta as together representing a ventral vessel, the afferent and efferent branchial arteries as commissural vessels, and the lateral veins as lateral vessels. It will be seen that the heart of Vertebrates is a muscular dilatation of the ventral vessel.

The blood is red, the colour being due, as in some species of Polygordius (p. 280), to hæmoglobin. The pigment is not, however, diffused in the plasma of the blood, but is confined to the *red corpuscles*, flattened oval cells with large nuclei, like those of the frog referred to in an early Lesson (p. 56, Fig. 8). Among the red corpuscles, but in much smaller numbers, are leucocytes. When the blood is fully oxygenated it takes on a bright scarlet colour, and is usually called *arterial blood*; when the oxygen has been given up to the tissues the colour becomes dull purple, and the blood is called *venous*. But the student must avoid the common error that arterial blood is necessarily confined to arteries and venous to veins; in the dogfish, for instance, the ventral aorta and the afferent branchial arteries contain venous blood.

In addition to the blood-vessels the dogfish possesses a set of channels called *lymphatics* (Fig. 104A, *ly*), consisting of colourless thin-walled vessels, mostly running alongside the arteries and veins. Traced in one direction they ramify extensively, and end in a set of *lymph-capillaries* interwoven with, but distinct from, the blood-capillaries; traced in the other direction they join into larger and larger trunks, provided at intervals with valves, and finally open into the veins. The lymph-capillaries take up the drainage from the

tissues and pass it into the veins. The fluid they contain, called *lymph*, is practically blood, *minus* its red corpuscles; its leucocytes are formed in structures called *lymphatic glands*, which occur in the course of the vessels. The lymphatics of the enteric canal are called *lacteals;* they take an important share in the absorption of fats.

The *nervous system*, like the circulatory organs, is vastly in advance of anything we have yet met with. The central nervous system consists of a *brain* (Fig. 103), contained in the cranial cavity, and continuous posteriorly with a *spinal cord* (*sp. c*) contained in the neural canal of the backbone. Thus the central nervous system is exclusively dorsal in position, and is not traversed by the enteric canal as in Polygordius, the crayfish, and the mussel.

Another characteristic feature of the dogfish's nervous system is that it is not solid, like that of Polygordius and the crayfish, but is tubular, being traversed by a longitudinal canal, the *neurocœle* (Fig. 99, *N. Cœ*), lined with epithelium. In the spinal cord the neurocœle has the form of a narrow *central canal;* in the brain it expands into a fairly capacious system of cavities, the *cerebral ventricles*.

The brain or anterior expansion of the nervous system is a complex structure divisible into several parts. The hindmost division, continuous with the spinal cord, is the *medulla oblongata* (Figs. 103 and 105, *NH*), and has above it the *cerebellum* (*HH*). Immediately in front of these two divisions is the *mid-brain*, produced above into paired elevations, the *optic lobes*. In front of the mid-brain is a small section called the *diencephalon* (*ZH*), and anterior to this again a large *prosencephalon* (*VH*), corresponding with the cerebral hemispheres of the higher Vertebrata, and giving off in front paired *olfactory lobes* (*L. ol*). All these divisions of the brain contain ventricles (*F. rho*), varying considerably in

form and size. Connected with the dorsal region of the

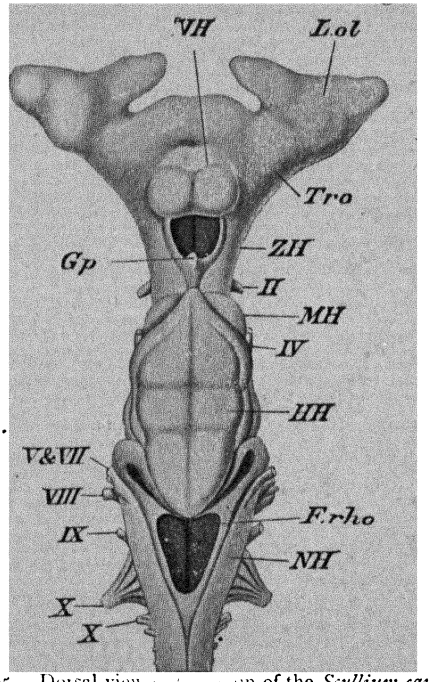

FIG. 105.—Dorsal view of the brain of the *Scyllium canicula*.

The posterior division of the brain is the medulla oblongata (*NH*), on the dorsal surface of which is shown one of the cerebral ventricles (*F. rho*).

The large cerebellum (*HH*) nearly covers the optic lobes (*MH*). The diencephalon (*ZH*) shows in the middle one of the cerebral ventricles, and the place of attachment of the pineal stalk (*Gp*).

The prosencephalon (*VH*) gives off the olfactory lobes (*Tro, L. ol.*).

The following nerves are shown :—optic (*II*), trochlear (*IV*), trigeminal (*V*), facial (*VII*), auditory (*VIII*), glossopharyngeal (*IX*), and vagus (*X*).

(From Wiedersheim.)

diencephalon is the *pineal body* (Fig. 103, *pin*), representing

the vestige of a sensory organ, and connected with the ventral surface of the same division is the *pituitary body* (*pty*).

The mode of origin of the nerves is also characteristic. From the spinal cord the nerves arise segmentally, one pair corresponding to each myomere, and pass through apertures in the neural arches of the vertebræ. Each arises by two roots, a dorsal and a ventral. The dorsal root is dilated into a ganglion, and contains only sensory fibres; the ventral root is non-ganglionated, and is motor. A longitudinal ganglionated *sympathetic nerve*, extending along the dorsal region of the cœlome, is connected with the spinal nerves, and sends branches to the viscera, blood-vessels, &c.

From the brain arise ten pairs of nerves, some of which are sensory, others motor, others mixed. Three are the nerves of the principal sense-organs, the first or *olfactory* supplying the organ of smell; the second or *optic* (Fig. 105, 11) the retina of the eye (*see* below), and the eighth or *auditory* (*VIII*), the organ of hearing. The third or *oculomotor*, the fourth or *trochlear* (*IV*), and the sixth or *abducent* go to the muscles of the eye; the fifth or *trigeminal* (*V*) to the snout and jaws; the seventh or *facial* (*VII*) to the palate, lower jaw, and hyoid arch; the ninth or *glossopharyngeal* (*IX*) to the hyoid and first branchial arches, and the tenth or *vagus* to the remaining branchial arches, as well as to the heart, stomach, and lateral line.

Besides the sensory tubes of the skin (lateral line, &c.), which are probably the seat of a delicate tactile sense, and the rudimentary tongue, which is presumably an organ of taste, there are three pairs of sensory organs, the structure and position of which is very characteristic of Vertebrates. These are the olfactory organs, the eyes, and the auditory organs.

The *olfactory organs* are a pair of cup-like sacs on the under side of the snout, enclosed in the olfactory capsules

and opening externally by the nostrils. They are lined with mucous membrane, which is raised up into ridges so as to increase the surface. The actual organ of smell is the epithelium forming the superficial layer of the mucous membrane ; it is developed as an in-pushing of the ectoderm, and is supplied by the olfactory nerve.

The *eyes* are a pair of nearly globular organs, lying in the orbits and moved each by six muscles. Their structure is, in all essential respects, the same as in man. There is an outer capsule, the *sclerotic*, formed of cartilage, lined by a vascular membrane, the *choroid*, within which is a delicate membrane, pigmented externally, the *retina* or actual organ of sight. In the front or exposed part of the eye the sclerotic passes into a transparent, watch-glass-like *cornea*, and the choroid into a curtain or diaphragm, the *iris*, having a central aperture, the *pupil*, to admit the rays of light to the interior of the eye. Behind the pupil is a gelatinous, biconvex *crystalline lens* of glassy transparency. The space between the cornea and the iris is called the *aqueous chamber* of the eye, and is filled by a watery fluid, the *aqueous humour*. The main part of the cavity of the eye, bounded in front by the lens, and for the rest of its extent by the retina, is the *vitreous chamber*, and is filled with a gelatinous substance, the *vitreous humour*. The cornea, aqueous humour, lens, and vitreous humour together form a series of adjustable lenses serving to focus objects on the retina, and the stimulus thus applied to that membrane is conveyed by the fibres of the optic nerve to the brain.

The auditory organ is a sac of complex form, the *membranous labyrinth*, enclosed in the auditory capsule of the skull, where it floats in a watery fluid, the *perilymph*. It consists of a sac called the *vestibule*, with which are connected three tubes, called from their form the *semicircular*

canals. Two of these, the anterior and posterior canals, are vertical in position, and are united with one another at their adjacent ends; at the other end each is dilated to form a bulb-like swelling, the *ampulla.* The third or horizontal canal opens at each end into the vestibule, and has an ampulla at its anterior end. The vestibule gives off a tube, the *endolymphatic duct*, which opens on the top of the head. The whole apparatus contains a fluid, the *endolymph*, in which is a gelatinous substance enclosing calcareous particles or *otoliths.* Patches of sensory epithelium are found in the vestibule and in the ampullæ, and to these the fibres of the auditory nerve are distributed. There seems little doubt that the membranous labyrinth has not only an auditory, but also an equilibrating function—*i.e.*, that the fish is enabled by its means to maintain its equilibrium in the water, as is also the case with the statocysts of Invertebrates.

The excretory and the reproductive organs of the dogfish are so closely associated as to be spoken of together as the *urinogenital organs.* The sexes are distinct, and the males are distinguished externally by having a pair of large grooved rods, the *claspers*, connected with the inner borders of the pelvic fins. They are used, like the peculiarly modified first and second pairs of pleopods in the male crayfish (p. 323), as copulatory organs.

The *kidneys* (Fig. 103, *kd*) are long, flat, lobulated bodies lying one on each side of the backbone in the posterior part of the abdominal cavity. From the ventral surface of each spring numerous delicate ducts or *ureters* (*ur*), some of which unite, opening into a small unpaired chamber, called in the female the *urinary sinus* and in the male the *urinogenital sinus* (*u. g. s*), which opens into the cloaca.

In the embryo the kidneys appear in the form of separate segmentally arranged tubes (Fig. 99, *Nph*) having the

general character of nephridia, opening on the one hand by nephrostomes into the cœlome, and on the other into a longitudinal duct which discharges into the cloaca. Thus the primitive structure of the kidney furnishes another instance of metamerism in the dogfish.

In the male there is a single pair of *spermaries* (Fig. 103, *ts*), in the form of large soft organs, united with one another posteriorly. They are suspended by a fold of peritoneum to the dorsal body-wall. From the anterior end of each arise numerous delicate *efferent ducts*, which enter a long, convoluted *spermiduct* or *vas deferens* (*v. def*). This passes along the ventral aspect of the kidneys and dilates into a conical pouch, the vesicula seminalis (*vs. sem*), and the two vesiculæ open, along with the ureters and a pair of reservoirs called sperm-sacs (*sp. s*), into the urinogenital sinus.

The female has a single *ovary* (Fig. 99, *ovy*) suspended to the dorsal body-wall by a fold of peritoneum. In the adult it is studded all over with rounded projections, the *ova*, varying in diameter from 12–14 mm. downwards. The oviducts (*ovd*) are paired and extend along the whole length of the dorsal wall of the cœlome, below the kidneys. Anteriorly they unite with one another below the gullet and just in front of the liver, and at the point of junction is a single aperture of considerable size (*ovd*), by which both tubes communicate with the cœlome: posteriorly they open into the cloaca. About the anterior third of each oviduct is narrow; its posterior two-thirds is wide and distensible, and at the junction of the two parts is a yellowish, glandular mass, the *shell-gland.*

Internal impregnation takes place, the spermatic fluid of the male being passed, by means of the claspers, into the oviducts of the female. The eggs, when ripe, break loose from the surface of the ovary into the cœlome, and thence pass, through the common aperture, into one or other of

the oviducts, where fertilisation occurs. As it passes into the dilated portion of the oviduct the oosperm of Scyllium becomes surrounded by a horn-like egg-shell or "mermaid's purse" secreted by the shell-gland, and having the form of a pillow-case produced at each of its four angles into a long, tendril-like process. The eggs are laid among sea-weed, to which they become attached by their tendrils. In Acanthias and Mustelus a mere vestige of the egg-shell is formed, and the eggs undergo the whole of their development in the

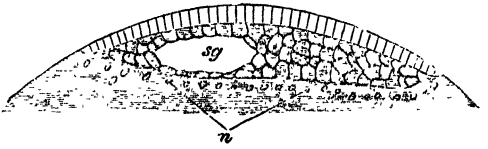

FIG. 106.—Section of the upper part of the embryo of a Dogfish in the blastula stage.

The blastoderm is formed of a single layer of ectoderm cells (white) and of several rows of cells (shaded), which subsequently give rise to endoderm and mesoderm: *sg.*, the blastocœle.

Below the blastoderm is the unsegmented yolk containing scattered nuclei (*n*).

(From Balfour.)

oviducts, the young being eventually born alive with the form and proportions of the adult.

The great size of the egg is due to the immense quantity of yolk it contains: its protoplasm is almost entirely aggregated at one pole in the form of a small disc. When segmentation of the oosperm takes place it affects the protoplasm alone, the inactive yolk, as in the Crayfish (p. 344), taking no part in the process. The polyplast stage consequently consists of a little heap of cells, called the *blastoderm* (Fig. 106), at one pole of an undivided

sphere of yolk. The edge of the blastoderm becomes invaginated at one point (gastrula-stage, p. 295) and its cells become differentiated into the three embryonic layers—ectoderm, mesoderm, and endoderm. At the same time the blastoderm extends in a peripheral direction so as gradually to cover the yolk, and its middle part becomes raised up into a ridge-like thickening which is moulded,

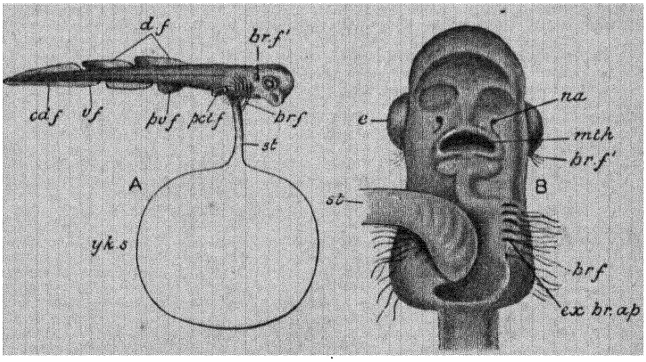

FIG. 107.—A, embryo of Scyllium with yolk-sac (× 1½): B, under-side of head, enlarged

br. f, branchial filaments protruding through gill-clefts: *br. f'*, branchial filaments protruding through spiracle; *cd. f*, caudal fin; *d. f*, dorsal fins; *e*, eye; *ex. br. ap*, external branchial apertures; *mth*, mouth; *na*, nostrils; *pc. f*, pectoral fin; *pv. f*, pelvic fin; *st*, yolk-stalk; *v. f*, ventral fin; *yk. s*, yolk-sac.

(After Balfour, slightly altered.)

step by step, into the form of the embryo fish. The head, trunk, and tail acquire distinctness, and become more and more clearly separated off from the bulk of the egg, the latter taking the form of a *yolk-sac* (Fig. 107, A, *yk. s*) attached by a narrow stalk to the ventral surface of the embryo.

In this condition the various parts of the adult fish can

be recognized, but the proportions are different, and the head presents several peculiarities. The gill-filaments (*br. f*) are so long as to project through the external branchial apertures and the spiracle (*br. f'*), in the form of long threads, abundantly supplied with blood-vessels, and apparently serving for the absorption of nutriment—the albumen in the egg-shell in the case of Scyllium, secretions of the oviduct in the viviparous forms. Besides this mode of nutrition the yolk-sac communicates with the intestine by a narrow duct (*st*), through which absorption of its contents is constantly going on. By the time the young fish is ready to be hatched or born the greater part of the yolk-sac has been drawn into the cœlome, a mere vestige of it still dangling from the ventral surface of the body.

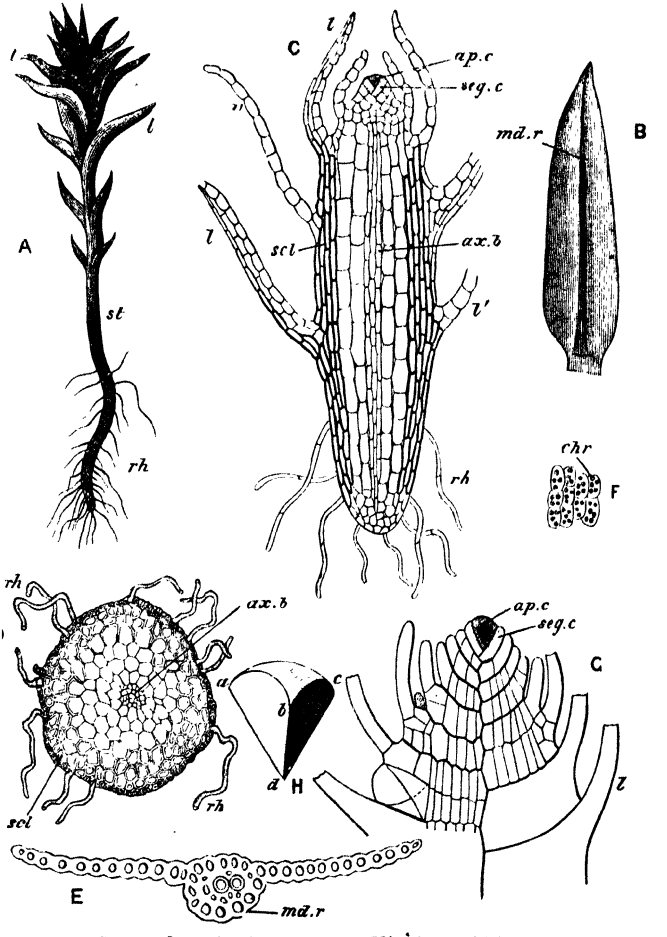

FIG. 108.—The Anatomy and Histology of Mosses.

A, Entire plant of *Funaria hygrometrica*, showing stem (*st*), leaves (*l*), and rhizoids (*rh*). (× 6.)

B, leaf of the same, showing midrib (*md. r*) and lateral portions. (× 25.)

LESSON XXX

MOSSES

In the six previous lessons we have traced the advance in organization of animals from the simple diploblastic Hydra to the complicated triploblastic forms which constitute the five higher phyla of the animal kingdom. We have now to follow in the same way the advance in structure of plants. The last member of the vegetable kingdom with which we were concerned was Nitella (Lesson XX), a solid aggregate, exhibiting a certain differentiation of form and structure, but yet composed of what were clearly recognizable as cells, there being, as in Hydra, none of those well-marked tissues which form so noticeable a feature in Polygordius as in other animals above the Cœlenterata.

Taking Nitella as a starting point, we shall see that among plants, as among animals, there is an increasing differentiation in structure and in function as we ascend the series. The first steps in the process are well illustrated by a consideration of that very abundant and beautiful group of plants, the Mosses. In spite of the variations in detail met with in different genera of the group, the essential features of their organization are so constant that the following description will be found to apply to any of the common forms.

C, semi-diagrammatic vertical section of a moss, showing the arrangement of the tissues. The stem is formed externally of sclerenchyma (*scl*), and contains an axial bundle (*ax. b*): in some of the leaves (*l*) the section passes through the midrib, in others (*l'*) through the lateral portion: the stem ends distally in an apical cell (*ap. c*), from which segmental cells (*seg. c*) are separated.

D, transverse section of the stem of *Bryum roseum*, showing sclerenchyma (*scl*), axial bundle (*ax. b*), and rhizoids (*rh*). (× 60.)

E, transverse section of a leaf of *Funaria*, showing the midrib (*md. r*) formed of several layers of cells, and the lateral portions one cell thick. (× 150.)

F, small portion of the lateral region of the same, showing the form of the cells and the chromatophores (*chr*). (× 150.)

G, distal end of the stem of *Fontinalis antipyretica* in vertical section, showing the apical cell (*ap. c*) giving rise to segmental cells (*seg. c*), which by subsequent division form the segments of the stem with the leaves: the thick lines show the boundaries of the segments.

H, diagram of the apical cell of a moss in the form of a tetrahedron with rounded base *abc* and three flat sides *abd*, *bcd*, *acd*.

(D, after Sachs; G, after Leitgeb.)

The plant consists of a short slender stem (Fig. 108, A, *st*), from which are given off structures of two kinds, rhizoids or root-hairs (*rh*), which pass downwards into the soil, and leaves (*l*), which are closely set on the stem and its branches. As in Nitella (p. 205) the portion of the stem from which a leaf arises is called a node, and the part intervening between any two nodes an internode, while the name segment is applied to a node with the internode next below it. At the upper or distal end of the stem the leaves are crowded, forming a terminal bud.

Owing to the opacity of the stem, its structure can only be made out by the examination of thin sections (C and D). It is a solid aggregate of close-set cells which are not all alike, but exhibit a certain amount of differentiation. In the outer two or three rows the cells (*scl*) are elongated in the direction of the length of the stem, so as to have a spindle-shape, and their walls are greatly thickened and of a reddish colour. They thus form a protective and supporting tissue, to which the name *sclerenchyma* is applied. Running longitudinally

through the centre of the stem is a mass of tissue (*ax. b*) distinguished by its small, thin-walled cells, and constituting the *axial bundle.*

The leaves (B) are shaped like a spear-head, pointed distally, and attached proximally by a broad base to the stem. The axial portion (B and E, *md. r*, C, *l*) consists of several layers of somewhat elongated cells and is called the *midrib:* the lateral portions (E and F: C, *l'*) are formed of a single layer of short cells. Thus the leaf has, for the most part, the character of a superficial aggregate. The cells contain oval chromatophores (F, *chr*).

The rhizoids (C and D, *rh*) are linear aggregates, being formed of elongated cells, devoid of chlorophyll, arranged end to end.

In the terminal bud the leaves, as in Nitella (pp. 206 and 208), arch over the growing point of the stem, which in this case also is formed of a single apical cell (C and G, *ap. c*). But in correspondence with the increased complexity of the plant, the apical cell is not a hemisphere from which new segments are cut off parallel to its flat base, but has the form (H) of an inverted, three-sided pyramid or tetrahedron, the rounded base of which (*abc*) forms the apex of the stem while segments (*seg. c*) are cut off from each of its three triangular sides in succession.

The best way to understand the apical growth of a moss is to cut a tetrahedron with rounded base out of a carrot or turnip: this represents the apical cell (H): then cut off a slice parallel to the side *abd*, a second parallel to *bcd*, and a third parallel to *acd:* these represent three successively formed segments. Now imagine that after every division the tetrahedron grows to its original size, and a very fair notion will be obtained of the way in which the successive segments of the moss-stem are formed by the fission in three

planes of the apical cell. Each segment (C and G, *seg. c*) immediately after its separation divides and subdivides, producing a mass of cells from which a projection grows out forming a leaf, and in this way the stem increases in length and the leaves in number.

Asexual reproduction takes place in various ways; all of them are, however, varieties of budding, and the buds always arise in the form of a linear aggregate of cells called a *protonema:* from this the moss-plant develops in the same way as from the protonema arising from a spore (p. 408).

The gonads are developed at the extremity of the main stem or one of its branches, and are enclosed in an *involucre* or tuft of leaves often of a reddish colour—the terminal bud of the fertile shoot or so-called "flower" of the moss.

The spermary (Fig. 109, A^1, A^2) is an elongated club-shaped body consisting of a solid mass of cells, the outermost of which form the wall of the organ, while the inner (A^3) become converted into sperms. The latter (A^4) are spirally coiled and provided with two cilia: they are liberated by the rupture of the wall of the spermary at its distal end (A^2), and swim in the rain or dew covering the plant.

The ovaries[1] (see Preface, p. viii) (B^1, B^2) may or may not occur on the same plant as the spermaries, some mosses being monœcious, others dicœcious. Like the spermaries, they consist at first of a solid mass of cells which assumes the form of a flask, having a rounded basal portion or *venter* (*v*) and a long *neck* (*n*). The outer layer of cells in the neck and the two outer layers in the venter form the wall of the ovary, the internal cells are arranged in a single

[1] **The ovary of mosses, ferns, &c., is usually called an *archegonium*: the spermary, as in the lower plants, an antheridium.**

axial row at first similar to those of the wall. As the ovary develops, the proximal or lowermost cell of the axial row takes on the character of an ovum (B^2, *ov*); the others, called *canal cells* (*cn. c*), are converted into mucilage, which by its expansion forces open the mouth of the flask and thus makes a clear passage from the exterior to the ovum (B^3).

Through the passage thus formed a sperm makes its way and conjugates with the ovum, producing as usual an oosperm or unicellular embryo.

The development of the embryo is at first remarkably like what we have found to take place in Hydroids (p. 246). The oosperm, having surrounded itself with a cell-wall, divides into two cells by a wall at right angles to the long axis of the ovary: each of these cells divides again repeatedly, and there is produced a solid multicellular embryo or *polyplast* (C^1, *spgnm*).

Very early, however, the moss-polyplast exhibits a striking difference from the animal polyplast or morula: one of its cells—that nearest the neck of the ovary—takes on the character of an apical cell, and begins to form fresh segments like the apical cell of the stem. Thus the plant embryo differs almost from the first from the animal embryo. In the animal there is no apical cell: all the cells of the polyplast divide and take their share in the formation of the permanent tissues. In the plant one cell is at a very early period differentiated into an apical cell, and from it all cells thereafter produced are, directly or indirectly, derived.

The embryo continues to grow, forming a long rod-like body (C^2, *spgnm*) the base of which becomes sunk in the tissue of the moss-stem, while its distal end projects vertically upwards, covered by the distended venter (*v*) of the ovary. Gradually it elongates more and more and its distal end

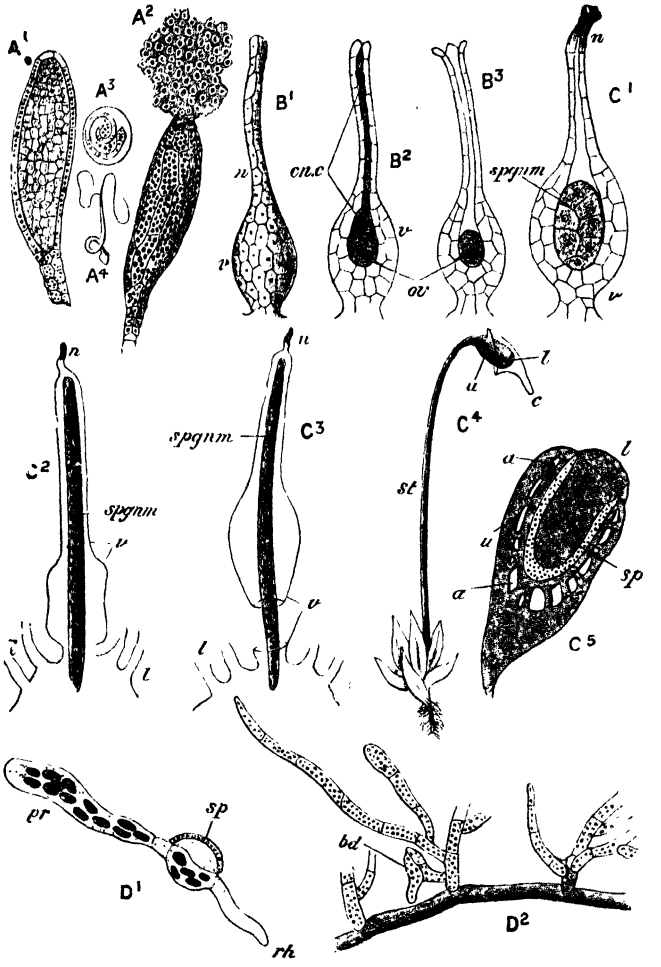

FIG. 109.—Reproduction and Development of Mosses.

A[1], A spermary of Funaria in optical section, showing the wall enclosing a central mass of sperm-cells: A[2], the same from the surface discharging its sperms. (× 300.)

A³, a sperm-cell with enclosed sperm: A⁴, a free-swimming sperm. (× 800.)

B¹, an ovary of Funaria, surface view, showing venter (*v*) and neck (*n*): B², the same in optical section, showing ovum (*ov*) and canal cells (*cn. c*): B³, the same after disappearance of the canal cells: the neck is freely open, and the ovum (*ov*) exposed. (× 200.)

C¹, ovary with withered neck containing an embryo (*spgnm*) in the polyplast stage (× 200): in C² the ovary, consisting of swollen venter (*v*) and shrivelled neck (*n*), encloses a young sporogonium (*spgnm*); the distal end of the stem is shown with bases of leaves (*l*); in C³ the venter has ruptured, forming a proximal portion or sheath and a distal portion or calyptra which is carried up by the growth of the sporogonium. (× 10.)

C⁴, a small plant of Funaria with ripe sporogonium consisting of seta (*st*), with urn (*u*) and lid (*l*) covered by the calyptra (*c*).

C⁵, diagrammatic vertical section of urn (*u*), showing lid (*l*), air spaces (*a*), and spores (*sp*).

D¹, a germinating spore of Funaria, showing ruptured outer coat (*sp*) and young protonema (*pr*) with rhizoid (*rh*). (× 550.)

D², portion of protonema of the same, showing lateral bud (*bd*), from which the leafy plant arises. (× 90.)

(A and D, after Sachs; B, C¹, and C⁵, altered from Sachs.)

dilates: the embryo has now become a *sporogonium*, consisting of a slender stalk (C⁴, *st*) bearing a vase-like capsule or urn (*u*) at its distal end. In the meantime the elongation of the stalk has caused the rupture of the enveloping venter of the ovary (C³): its proximal part remains as a sort of sheath round the base of the stalk, while its distal portion, with the shrivelled remains of the neck (*n*), is carried up by the elongation of the sporogonium and forms an extinguisher-like cap or *calyptra* (C⁴, *c*) over the urn.

As development goes on, the distal end of the urn becomes separated in the form of a lid (C⁴, C⁵, *l*), and certain of the cells in its interior, called *spore-mother cells*, divide each into four daughter cells, which acquire a double cell-wall and constitute the *spores* (C⁵, *sp*) of the moss.

When the spores are ripe the calyptra falls off or is blown away by the wind, the lid separates from the urn, and the spores are scattered.

In germination, the protoplasm of the spore covered by

the inner layer of the cell-wall protrudes through a split in the outer layer (D^1, *sp*) and grows into a long filament, the *protonema* (*pr.*), divided by oblique septa into a row of cells. The protonema—which it will be observed is a simple linear aggregate—branches, and may form a closely-matted mass of filaments. Sooner or later small lateral buds (D^2, *bd*) appear at various places on the protonema: each of these takes on the form of a three-sided pyramidal apical cell, which then proceeds to divide in the characteristic way (p. 403), forming three rows of segments from which leaves spring. In this way each lateral bud of the protonema gives rise to a moss-plant.

Obviously we have here a somewhat complicated case of alternation of generations (see p. 248). The gamobium or sexual generation is represented by the moss-plant, which originates by budding and produces the sexual organs, while the agamobium consists of the sporogonium, developed from the oosperm and reproducing by means of spores. The protonema, arising from a spore and producing the leafy plant by budding, is merely a stage of the gamobium.

The nutrition of mosses is holophytic; but there is a striking differentiation of function correlated with terrestrial habits. In Nitella the entire organism is submerged in water and all the cells contain chlorophyll, so that decomposition of carbon dioxide and absorption of an aqueous solution of salts are performed by all parts alike, every cell being nourished independently of the rest. In the moss, on the other hand, the rootlets are removed from the influence of light and contain no chlorophyll: hence they cannot decompose carbon dioxide; but, being surrounded by moist soil, are in the most favourable position for absorbing water and mineral salts. The stem, again, is

converted into an organ of support: the thickness of its external cells prevents absorption and it contains no chlorophyll. Hence the function of decomposing carbon dioxide is confined to the leaves.

We have thus as an important fact in the nutrition of an ordinary terrestrial plant that its carbon is taken in at one place, its water, nitrogen, sulphur, potassium, &c., at another. But as all parts of the plant require all these substances it is evident that there must be some means by which the root can obtain a supply of carbon, and the leaves a supply of elements other than carbon. In other words, we find for the first time in the ascending series of plants, just as we did in ascending from the simple Hydra to the complex Polygordius (p. 278) the need for some contrivance for the distribution of food-materials.

The way in which this distributing process is performed has been studied chiefly in the higher plants, but its essential features are probably the same for mosses.

Water is continually evaporating from the surface of the leaves, its place being as constantly supplied by water—with salts in solution—taken in by the rhizoids. This *transpiration*, or giving off of water from the leaves, is one important factor in the process under consideration, since it ensures a constant upward current of water, or, more accurately, of an aqueous solution of mineral salts. The withering of a plucked moss-plant is of course due to the fact that when the roots are not embedded in moist soil or in water, transpiration is no longer balanced by absorption.[1] In the higher plants it has been found that the root-hairs have an absorbent action independent of transpiration, so that water may be absorbed in the absence of leaves.

[1] Mosses, however, unlike most higher plants, can absorb water by their leaves.

By the transpiration current, then, the leaves are kept constantly supplied with a solution of mineral salts derived from the soil, and are thus nourished like any of the aquatic green plants considered in previous lessons: by the double decomposition of water and carbon dioxide a carbo-hydrate is formed: this, by further combination with the nitrogen of the absorbed ammonium salts or nitrates, forms simple nitrogenous compounds, and from these, probably through a long series of mesostates or intermediate products, protoplasm is finally manufactured.

In this way the food supply of the green cells of the leaves is accounted for, but we have still to consider that of the colourless cells of the stem and rhizoids, which, as we have seen, are supplied by the transpiration current with everything they require except carbon, and this, owing to their possessing no chlorophyll, they are unable to take in in the form of carbon dioxide.

As a matter of fact the chlorophyll-containing cells of the leaves have to provide not only their own food, but also that of their not-green fellows. In addition to making good the waste of their own protoplasm they produce large quantities of plastic products (see p. 33) such as grape sugar, and simple nitrogenous compounds like asparagin, and these pass by diffusion from cell to cell until they reach the uttermost parts of the plant, such as the axis of the stem and the extremities of the rhizoids. The colourless cells are in this way provided not only with the salts contained in the ascending transpiration current, but with carbo-hydrates and nitrogenous compounds. From these they derive their nutriment, living therefore like yeast-cells in Pasteur's solution, or like Bacteria in an organic infusion.

We see then that the colourless cells of the stem and

rhizoids are dependent upon the green cells of the leaves for their supplies. Like other cells devoid of chlorophyll they are unable to make use of carbon dioxide as a source of carbon, but require ready-made carbo-hydrates, the manufacture of which is continually going on, during daylight, in the chlorophyll-containing cells of the leaves. This striking division of labour is the most important physiological difference between mosses and the more lowly organised green plants described in previous lessons.

LESSON XXXI

FERNS

We saw in the previous lesson that in mosses there is a certain though small amount of histological differentiation, some cells being modified to form sclerenchyma, others to form axial bundles. We have now to consider a group of plants which may be considered to be, in this respect, on much the same morphological level as Polygordius, the adult organism being composed not of a mere aggregate of simple cells, but of various well-marked tissues.

A fern-plant has a strong stem which in some forms, such as the common Bracken (*Pteris aquilina*) is a horizontal underground structure called a *rhizome*, often incorrectly considered as a root: in others it creeps over the trunks of trees or over rocks: in others again, such as the tree-ferns, it is vertical, and may attain a height of three or four metres. From the stem are given off structures of two kinds—the leaves, which present an almost infinite variety of form in the various species, and the numerous slender roots. In some cases, such as the tree-ferns and the common Male Shield-fern (*Aspidium filix-mas*), the plant ends distally in a terminal bud, consisting, as in Nitella and mosses, of the growing end of the stem over-arched by leaves: in others

such as Pteris, the stem ends in a blunt, knob-like extremity quite uncovered by leaves. On the proximal portion of the stem are usually found the withered remains of the leaves of previous seasons, or the scars left by their fall. The roots are given off from the whole surface of the stem, often covering it with a closely-matted mass of dark brown fibres.

When the stem is cut across transversely (Fig. 110, A) it is seen, even with the naked eye, to consist of three well marked tissues. The main mass of it is formed of a whitish substance, soft and rather sticky to the touch, and called *ground-parenchyma* (*par*): this is covered by an external layer of very hard tissue, dark brown or black in colour, the *hypodermis* (*hyp*): bands of a similar hard brown substance are variously distributed through the parenchyma, and constitute the *sclerenchyma* (*scl*): and interspersed with these are rounded or oval patches of a yellowish colour (*V.B*) harder than the parenchyma but not so hard as the sclerenchyma, and called *vascular bundles*.

The general distribution of these tissues can be made out by making longitudinal sections of the stem in various planes or by cutting away the hypodermis, and then scraping the parenchyma from the vascular bundles and bands of sclerenchyma. The hypodermis is found to form a more or less complete hard sheath or shell to the stem, while the sclerenchyma and vascular bundles form longitudinal bands and rods imbedded in the parenchyma, and serve as a sort of supporting framework or skeleton.

The minute structure of the stem can be made out by the examination either of very thin longitudinal and transverse sections, or of a bit of stem which has been reduced to a pulp by boiling in nitric acid with the addition of a few crystals of potassium chlorate: by this process the various

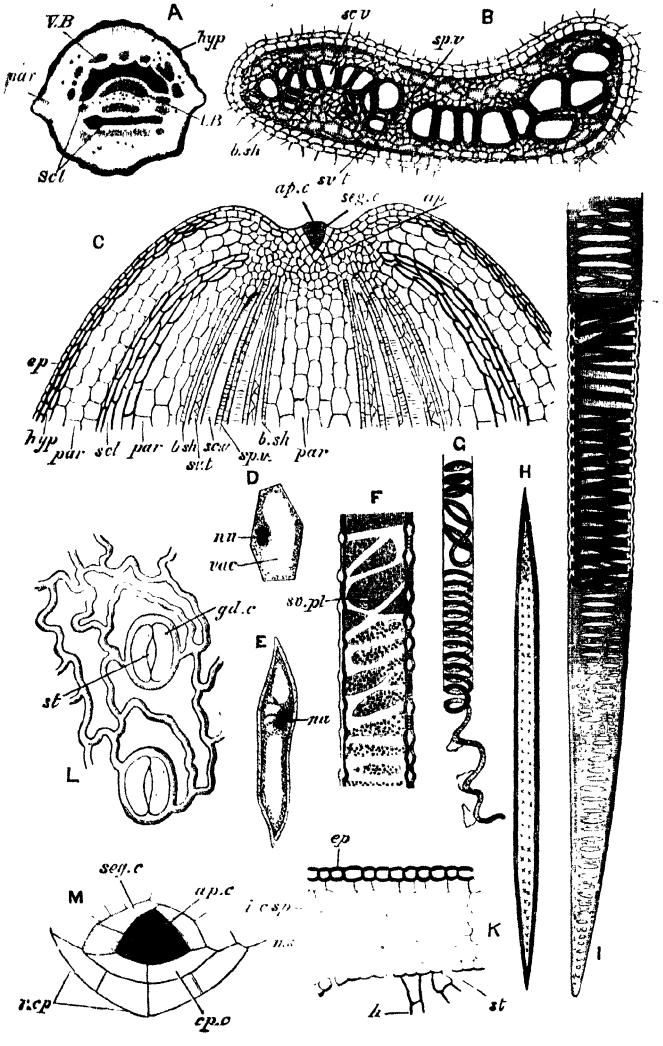

FIG. 110. —Anatomy and Histology of Ferns.

A, Transverse section of the stem of *Pteris aquilina*, showing hypodermis (*hyp*), ground-parenchyma (*par*), sclerenchyma (*scl*), and vascular bundles (*V. B*). (× 2.)

B, transverse section of a vascular bundle, showing bundle-sheath (*b. sh*), sieve-tubes (*sv. t*), scalariform vessels (*sc. v*), and spiral vessels (*sp. v*). (× 6.)

C, semi-diagrammatic vertical section of the growing point of the stem, showing apical cell (*ap. c*), segmental cells (*seg. c*), and apical meristem (*ap. mer*) passing into permanent tissue consisting of epidermis (*ep*), hypodermis (*hyp*), ground parenchyma (*par*), sclerenchyma (*scl*), and vascular bundles in which the sheath (*b. sh*), sieve-tubes (*sv. t*), scalariform vessels (*sc. v*), and spiral vessels (*sp. v*) are indicated.

D, a single parenchyma cell, showing nucleus (*nu*), and vacuole (*vac*).

E, cell of hypodermis.

F, portion of a sieve-tube, showing sieve-plates (*sv. pl*).

G, portion of a spiral vessel with the spiral fibre partly unrolled at the lower end.

H, fibre-like cell of sclerenchyma.

I, portion of a scalariform vessel, part of the wall being supposed to be removed.

K, vertical section of a leaf of Pteris, showing upper and lower epidermis (*ep*), mesophyll cells (*ms. ph*), with intercellular spaces (*i. c. sp*), a stoma (*st*) in the lower epidermis, and hairs (*h*).

L, surface view of epidermis of leaf of Aspidium, showing two stomata (*st*) with their guard-cells (*gd. c*).

M, vertical section of the end of a root, showing apical cell (*ap. c*), segmental cells (*seg. c*), and root-cap (*r. cp*) with its youngest cap-cells marked *cp. c*.

(A, B, and D–K after Howes; M from Sachs, slightly altered.)

tissue elements are separated from one another, and can be readily examined under a high power.

By combining these two methods of sectioning and dissociation, the parenchyma is found to consist of an aggregate of polyhedral cells (C, *par*; D) considerably longer than broad, their long axes being parallel with that of the stem itself. The cells are to be considered as right cylinders which have been converted into polyhedra by mutual pressure. They have the usual structure, and their protoplasm is frequently loaded with large starch-grains. They do not fit quite closely together, but spaces are left between them, especially at the angles, called *intercellular spaces*.

The cells of the hypodermis (E) are proportionally longer than those of the parenchyma, and are pointed at each end: they contain no starch. Their walls are greatly thickened, and are composed not of cellulose but of *lignin*, a carbohydrate allied in composition to cellulose, but containing a larger proportion of carbon. Schulze's solution, which, as we have seen, stains cellulose blue, imparts a yellow colour to lignin.

Outside the hypodermis is a single layer of cells (C, *ep*) not distinguishable by the naked eye and forming the actual external layer of the stem: the cells have slightly thickened, yellowish-brown walls, and constitute the *epidermis*. From many of them are given off delicate filamentous processes consisting each of a single row of cells: these are called *hairs*.

In the sclerenchyma the cells (H) are greatly elongated, and pointed at both ends, so as to have the character rather of fibres than of cells. Their walls are immensely thickened and lignified, and present at intervals oblique markings due to narrow but deep clefts: these are produced by the deposition of lignin from the surface of the protoplasm (see p. 33) being interrupted here and there, instead of going on continuously as in the case of a cell-wall of uniform thickness.

The vascular bundles have in transverse section (B) the appearance of a very complicated network, with meshes of varying diameter. In longitudinal sections (C) and in dissociated specimens they are found to be partly composed of cells, but to contain besides structures which cannot be called cells at all.

In the centre of the bundle are a few narrow cylindrical tubes (B and C, *sp. v.*) characterised at once by a spiral marking, and hence called *spiral vessels*. Accurate examination shows that their walls (G) are for the most part thin,

but are thickened by a spiral fibre, just as a paper tube might be strengthened by gumming a spiral strip of pasteboard to its inner surface. These vessels are of considerable length, and are open at both ends: moreover they contain no protoplasm, but are filled with either air or water: they have therefore none of the characteristics of cells. They are shown, by treatment with Schulze's solution, to be composed of lignin.

Surrounding the group of spiral vessels, and forming the large polygonal meshes so obvious in a transverse section, are wide tubes (B and C, *sc. v*) pointed at both ends and fitting against one another in longitudinal series by their oblique extremities. They have transverse markings like the rungs of a ladder, and are hence called *scalariform vessels*. The markings (1) are due to wide transverse pits in the otherwise thick lignified walls: in the oblique ends by which the vessels fit against one another the pits are frequently replaced by actual slits, so that a longitudinal series of such vessels forms a continuous tube containing, like the spiral vessels, air or water, but no protoplasm. In most ferns the terminal walls are not thus perforated, and the elements are then called *tracheides*.

The presence of these vessels—spiral and scalariform—is the most important histological character separating ferns and mosses. The latter group and all plants below them are composed exclusively of cells: ferns and all plants above them contain vessels in addition, and are hence called *vascular plants*.

The vessels, together with small parenchyma-cells interspersed among them, make up the central portion of the vascular bundle, called the *wood* or *xylem*. The peripheral portion is formed of several layers of cells composing the *bast* or *phloëm*, and surrounding the whole are two layers of

small cells, the inner called the *phloëm-sheath* or *pericycle*, the outer, the *bundle-sheath* or *endodermis* (*b. sh*).

The cells of the phloëm are for the most part parenchymatous, but among them are some to which special attention must be drawn. These (B and C, *sv. t*), are many times as long as they are broad, and have on their walls irregular patches or *sieve-plates* (F, *sv. pl.*) composed of groups of minute holes through which the protoplasm of the cell is continuous with that of an adjacent cell. The transverse or oblique partitions between the cells of a longitudinal series are also perforated, so that a row of such cells forms a *sieve-tube* in which the protoplasm is continuous from end to end. We have here, therefore, as striking an instance of a non-cellular tissue as in the deric epithelium and certain other tissues of Polygordius (see p. 289).

The distal or growing end of the stem terminates in a blunt *apical cone* or punctum vegetationis (C), surrounded by the leaves of the terminal bud in the case of vertical stems, or sunk in a depression and protected by close-set hairs in the underground stem of the bracken. A rough longitudinal section shows that, at a short distance from the apical cone, the various tissues of the stem—epidermis, parenchyma, sclerenchyma, and vascular bundles—merge insensibly into a whitish substance, resembling parenchyma to the naked eye, and called *apical meristem* (*ap. mer*).

Thin sections show that the summit of the apical cone is occupied by a wedge-shaped apical cell (*ap. c*) which in vertical stems is three-sided like that of mosses (Fig. 108, H, p. 401), while in the horizontal stem of Pteris it is two-sided. As in mosses, segmental cells (*seg. c*) are cut off from the three (or two) sides of the apical cell in succession, and by further division form the apical meristem (*ap. mer*), which consists

of small, close-set cells without intercellular spaces. As the base of the apical cone is reached, the meristem is found to pass insensibly into the permanent tissues, the cells near the surface gradually merging into epidermis and hypodermis, those towards the central region into sclerenchyma and the various constituents of the vascular bundles, and those of the intermediate regions into parenchyma.

The examination of the growing end of the stem shows us how the process of apical growth is carried on in a complicated plant like the fern. The apical cell is continually undergoing fission, forming a succession of segmental cells; these divide and form the apical meristem, which is thus being constantly added to at the growing end by the formation and subsequent fission of new segmental cells: in this way the apex of the stem is continually growing upwards or forwards. But at the same time the meristem cells farthest from the apex begin to differentiate: some elongate but slightly, increasing greatly in size, and become parenchyma cells: others by elongation in the direction of length of the stem and by thickening and lignification of the cell-wall become sclerenchyma cells: others again elongate greatly, become arranged end to end in longitudinal rows, and, by the loss of their protoplasm and of the transverse partitions between the cells of each row, are converted into vessels—spiral or scalariform according to the character of their walls. Thus while the epidermis, parenchyma, and sclerenchyma are formed of cells, the spiral and scalariform vessels are *cell-fusions*, or more accurately cell-wall-fusions, being formed by the union in a longitudinal series of a greater or less number of cell-walls. It will be remembered that the muscle-plates of Polygordius are proved by the study of development to be cell-fusions (p. 302).

We thus see that every cell in the stem of the fern was

once a cell in the apical meristem, that every vessel has arisen by the concrescence of a number of such cells, and that the meristem cells themselves are all derived, by the ordinary process of binary fission, from the apical cell. In this way the concurrent processes of cell-division, cell-differentiation, and cell-fusion result in the production of the various and complex tissues of the fully-formed stem.

The leaves vary greatly in form in the numerous genera and species of ferns: they may consist of an unbranched *stalk* bearing a single expanded green *blade:* or the stalk may be more or less branched, its ramifications bearing the numerous subdivisions of the blade, or *pinnules.*

The anatomy of the leaf, like that of the stem, can be readily made out by a rough dissection. The leaf-stalk and its branches have the same general structure as the stem, consisting of parenchyma coated externally with epidermis and strengthened internally by vascular bundles, which are continuous with those of the stem. But the blade, or, in the case of a compound leaf, the pinna, has a different and quite peculiar structure. It is invested by a layer of epidermis which can be readily stripped off as an extremely thin, colourless membrane, exposing a soft, green substance, the leaf-parenchyma or *mesophyll.* The leaf is marked externally by a network of delicate ridges, the *veins;* these are shown by dissection to be due to the presence of fine white threads which ramify through the mesophyll, and can be proved by tracing them into the leaf-stalk to spring from its vascular bundles, of which they are in effect the greatly branched distal ends.

Microscopic examination shows the epidermis of the leaf (Fig. 110, K, *ep* and L) to consist of flattened, colourless cells of very irregular outline and fitting closely to one another like

the parts of a child's puzzle. Among them are found at intervals pairs of sausage-shaped cells (*gd. c*) placed with their concavities towards one another so as to bound a narrow slit-like aperture (*st*). These apertures, which are the only intercellular spaces in the epidermis, are called *stomates*: the cells bounding them are the *guard-cells*, and are distinguished from the remaining epidermic cells by the possession of a few chromatophores.

The mesophyll, which as we have seen occupies the whole space between the upper and lower epidermis, is formed of thin-walled cells loaded with chromatophores (K, *ms.ph*) and therefore of a deep green colour. The cells in contact with the upper epidermis are cylindrical, and are arranged vertically in a single row: those towards the lower surface are very irregular both in form and arrangement. Large intercellular spaces (*i. c. sp*) occur between the mesophyll-cells and communicate with the outer air through the stomates.

The leaves arise as outgrowths of the distal or growing end of the stem, each originating from a single segmental cell of the apical cone.

The fern is the first plant we have yet considered which possesses true roots, the structures so-called differing fundamentally from the simple rhizoids of Nitella and the mosses. Instead of being mere linear aggregates of cells, they agree in general structure with the stem from which they spring, consisting of an outer layer of epidermis within which is parenchyma strengthened by bands of sclerenchyma and by a single vascular bundle in the middle. The epidermic cells give rise to unicellular prominences, the *root-hairs*.

The apex of the root, like that of the stem, is formed of a mass of meristem in which a single wedge-shaped apical cell (Fig. 110, M, *ap. c*) can be distinguished But instead

of the base of this cell forming the actual distal extremity, as in the stem (compare c), it is covered by several layers of cells which constitute the *root-cap* (*r. cp*). In fact the apical cell of the root divides not only by planes parallel to its three sides, but also by a plane parallel to its base, and in this way produces not only three series of segmental cells (*seg. c*) which afterwards subdivide to form the apical meristem, but also a series of cap-cells (*cp. c*) which form a protective sheath over the tender growing end of the root as it forces its way through the soil.

Roots are also peculiar in their development. Instead of being, like leaves, prominences of the superficial tissues of the stem, they arise from a layer of cells immediately external to the vascular bundles, and in growing force their way through the superficial portion of the stem, through a fissure from which they finally emerge. They are thus said to be *endogenous* in origin while leaves are *exogenous*.

The nutrition of ferns is carried on in much the same way as in mosses (see p. 408). Judging from the analogy of flowering plants it would seem that the ascending current of water from the roots passes mainly through the xylem of the vascular bundles, while the descending current of nitrogenous and other nutrient matters for the supply of the colourless cells of the stem and roots passes chiefly through the phloëm and especially through the sieve-tubes. The absorption of water is effected by the root-hairs.

In the autumn there are found on the under surfaces of the leaves brown patches called *sori*, differing greatly in form and arrangement in the various genera, and formed of innumerable, minute, seed-like, bodies, the *sporangia* (Fig. 111, A), just visible to the naked eye. Each sorus or group

of sporangia is covered by a fold of the epidermis of the leaf, called the *indusium*.

A sporangium is attached to the leaf by a multicellular stalk (*st*), and consists of a sac resembling two watch-glasses placed with their concave surfaces towards one another and their edges united by a thick rim (*an*). The sides are formed of thin flattened cells with irregular outlines, the rim or *annulus* of peculiarly shaped cells which are thin and broad at one edge (to the left in A), but on the other (to the right) are thick, strongly lignified, and of a yellowish-brown colour. The whole internal cavity is filled with spores (B, *sp*) having the form of tetrahedra with rounded edges, and each consisting of protoplasm containing a nucleus, and surrounded by a double wall of cellulose. A spore is therefore, as in mosses, a single cell.

Each sporangium arises from a single epidermic cell of the leaf. This divides repeatedly so as to form a solid mass of cells, of which the outermost become the wall of the sporangium while the inner are the spore-mother-cells. The latter divide each into four spores, as in mosses (p. 407).

As the spores ripen, the wall of the sporangium dries, and as it does so the thickened part of the annulus straightens out, tearing the thin cells and producing a great rent through which the spores escape (B).

When the spores are sown on moist earth they germinate, the protoplasm, covered by the inner coat, protruding through the ruptured outer coat (C, *sp*) in the form of a short filament. This divides transversely, forming two cells, the proximal of which sends off a short rhizoid (*rh*). The resemblance of this stage to the young protonema of a moss is sufficiently obvious (see Fig. 109, D^1, p. 406).

Further cell-division takes place, and before long the

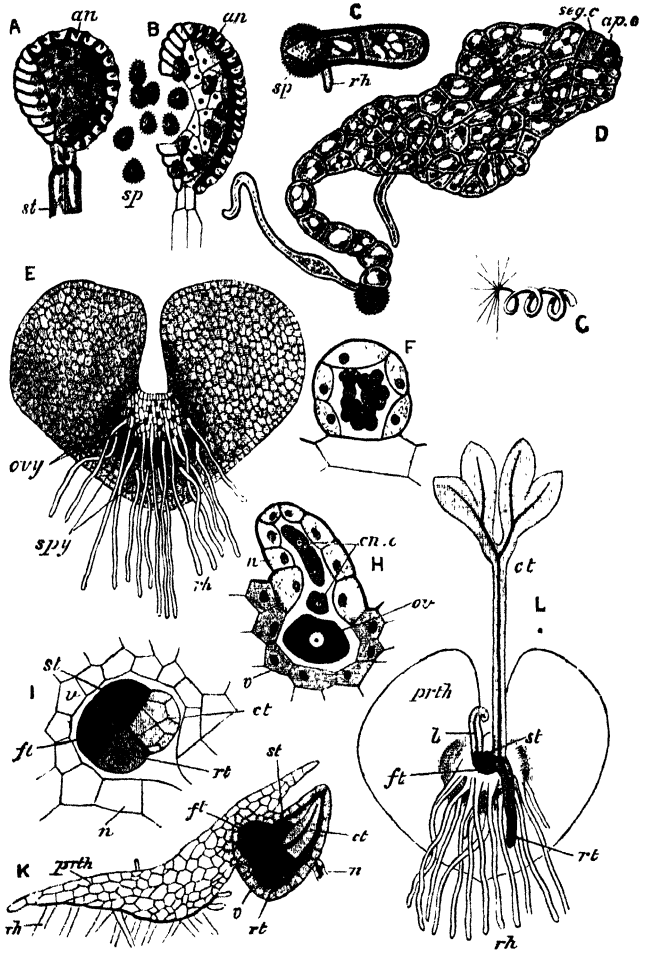

FIG. 111.—Reproduction and Development of Ferns.

A, Sporangium of *Pteris*, external view, showing stalk (*st*) and annulus (*an*).

B, the same, during dehiscence, the spores (*sp*) escaping.

C, a germinating spore, showing the ruptured outer coat (*sp*), and a

rhizoid (*rh*) springing from the proximal cell of the rudimentary (two-celled) prothallus.

D, a young prothallus, showing spore, rhizoid, apical cell (*ap. c*), and segmental cells (*seg. c*).

E, an advanced prothallus, from beneath, showing rhizoids (*rh*), ovaries (*ovy*), and spermaries (*spy*).

F, a mature spermary of *Pteris*, inverted (*i.e.* with its distal end directed upwards) so as to compare with Fig. 109, A.

G, a single sperm, showing coiled body and numerous cilia.

H, a mature ovary of *Aspidium*, inverted so as to compare with Fig. 109, B³, showing venter (*v*), neck (*n*), ovum (*ov*), and canal cells (*can. c*).

I, small portion of a prothallus of *Asplenium* in vertical section, showing the venter (*v*) and part of the neck (*n*) of a single ovary after fertilisation. The venter contains an embryo just passing from the polyplast into the phyllula stage, and divided into four groups of cells, the rudiments respectively of the foot (*ft*), stem (*st*), root (*rt*), and cotyledon (*ct*).

K, vertical section of a prothallus (*prth*) of *Nephrolepis*, bearing rhizoids (*rh*), and a single ovary with greatly dilated venter (*v*) and withered neck (*n*). The venter contains an embryo in the phyllula stage, consisting of foot (*ft*), rudiments of stem (*st*), and root (*rt*), and cotyledon (*ct*) beginning to grow upwards.

L, prothallus (*prth*) with rhizoids (*rh*), bearing a young fern-plant, consisting of foot (*ft*), rudiment of stem (*st*), first root (*rt*), cotyledon (*ct*), and first ordinary leaf (*l*). (After Howes.)

distal cells divide longitudinally, a leaf-like body being produced, which is called the *prothallus* (D). This is at first only one layer of cells thick, but it gradually increases in size, becoming more or less kidney-shaped (E), and as it does so its cells divide parallel to the surface, making it two and finally several cells in thickness. Thus the prothallus is at first a linear, then a superficial, and ultimately a solid aggregate. Root-hairs (*rh*) are produced in great number from its lower surface, and penetrating into the soil serve for the absorption of nutriment. At an early period a two-sided apical cell (D, *ap. c*) is differentiated, and gives off segmental cells (*seg. c*) in the usual way: an abundant formation of chromatophores also takes place at a very early period in the cells of the prothallus, which therefore resembles both in structure and in habit some very simple form of moss.

On the lower surface of the prothallus gonads (E, *spy*, *ovy*) are developed, resembling in their essential features those of mosses. The spermaries (*spy*) make their appearance first, being frequently found on very young prothalli. One of the lower cells forms a projection which becomes divided off by a septum: further division takes place, resulting in the differentiation (F) of an outer layer of cells forming the wall of the spermary, and of an internal mass of sperm-mother-cells in each of which a sperm is produced. The sperm (G) is a corkscrew-like body, probably formed from the nucleus of the cell, bearing at its narrow end a number of cilia which appear to originate from the protoplasm. To the thick end is often attached a globular body, also arising from the protoplasm of the mother-cell; this is finally detached.

The ovaries (E and H, *ovy*) are not usually formed until the prothallus has attained a considerable size. Each arises, like a spermary, from a single cell cut off by a septum from one of the lower cells of the prothallus: the cell divides and forms a structure resembling in general characters the ovary of a moss (see Fig. 109, B, p. 406), except that the venter (H, *v*) is sunk in the prothallus, and is therefore a less distinct structure than in the lower type. As in mosses, also, an axial row of cells is early distinguished from those forming the wall of the ovary: the proximal of these becomes the ovum (*ov*), the others are the canal-cells (*cn. c*), which are converted into mucilage, and by their expansion force open the neck and make a clear passage for the sperm.

The sperms swarm round the aperture of the ovary and make their way down the canal, one of them finally conjugating with the ovum and converting it into an oosperm.

The early stages in the development of the embryo remind us, in their general features, of what we found to occur in mosses (p. 405). The oosperm first divides by a

plane parallel to the neck of the ovary, forming two cells, an anterior nearest the growing or distal end of the prothallus, and a posterior towards its proximal end. Each of these divides again by a plane at right angles to the first, there being now an upper and a lower anterior, and an upper and a lower posterior cell: the lower in each case being that towards the downwardly directed neck of the ovary. Each of the four cells undergoes fission, the embryo then consisting of eight cells, two upper anterior (right and left), two lower anterior, two upper posterior, and two lower posterior. We thus get a multicellular but undifferentiated stage, the polyplast.

It will be remembered that in mosses the polyplast forms an apical cell, and develops directly into the sporogonium (p. 405). In the fern the later stages are more complex. One of the upper anterior cells remains undeveloped, the other (Fig. 111, I and K, *st*) takes on the form of a wedge-shaped apical cell, and, dividing in the usual way, forms a structure like the apex of the fern-stem, of which it is in fact the rudiment. The two upper posterior cells divide and subdivide, and form a multicellular mass called the *foot* (*ft*), which becomes embedded in the prothallus, and serves the growing embryo for the absorption of nutriment. One of the lower posterior cells remains undeveloped, the other (*rt*) takes on the form of the apical cell of a root, *i.e.*, of a wedge-shaped cell, which not only produces three sets of segmental cells from its sides but also cap-cells from its base (p. 422): division of this cell goes on very rapidly, and a *primary root* is produced which at once grows downwards into the soil. Finally the two lower anterior cells undergo rapid fission, and develop into the first leaf of the embryo, called the *cotyledon* (*ct*), which soon begins to grow upwards towards the light.

Thus at a comparatively early stage of its development the fern-embryo has attained a degree of differentiation far beyond anything which occurs in the moss-embryo. The scarcely differentiated polyplast has passed into a stage which may be called the *phyllula*, distinguished by the possession of those two characteristic organs of the higher plants, the leaf and root.

Notice how early in development the essential features of animal or plant manifest themselves. In Polygordius the polyplast is succeeded by a gastrula distinguished by the possession of a digestive cavity: in the fern no such cavity is formed, but the polyplast is succeeded by a stage distinguished by the possession of a leaf and root. In the one case the characteristic organ for holozoic, in the other the characteristic organs for holophytic nutrition make their appearance, and so mark the embryo at once as animal or plant. We may say then that while the oosperm and the polyplast stages of the embryo are common to the higher plants and the higher animals, the correspondence goes no further, the next step being the formation in the animal of an enteron, in the plant of a leaf and root. In other words the phyllula is the correlative of the gastrula.

The cotyledon increases rapidly in size, and emerges between the lobes of the kidney-shaped prothallus (L): the root at the same time grows to a considerable length, the result being that the phyllula becomes a very obvious structure in close connection with the prothallus, and indeed appearing to be part of it. The two are actually, however, quite distinct, their union depending merely upon the fact that the foot of the phyllula is embedded in the tissue of the prothallus like a root in the soil. Hence the phyllula is related to the prothallus in precisely the same way as the

sporogonium to the moss plant (compare Fig. 111, K, with Fig. 109, c^2, and Fig. 111, L, with Fig. 109, c^4).

The rudiment of the stem (L, *st*) continues to grow by the production of fresh segments from its apical cell: leaves (*l*) are developed from the segments, and grow upwards parallel with the cotyledon. The leaves first formed are small and simple in structure, but those arising later become successively larger and more complicated, until they finally attain the size and complexity of the ordinary leaves of the fern. In the meantime new roots are formed and the primary root ceases to be distinguishable; the cotyledon, the foot, and the prothallus wither, and thus the phyllula, by the successive formation of new parts from its constantly growing stem, becomes a fern-plant.

We see that the life-history of the fern resembles in essentials that of the moss. In both, alternation of generation occurs, a gamobium or sexual generation giving rise, by the conjugation of ovum and sperm, to an agamobium or asexual generation, which, by an asexual process of spore-formation, produces the gamobium. But in the relative proportions of the two generations the difference is very great. What we know as the moss plant is the gamobium, and the agamobium is a mere spore-producing structure, never getting beyond the stage of a highly differentiated polyplast, and dependent throughout its existence upon the gamobium, to which it is permanently attached. What we know as the fern plant is the agamobium, a large and complex structure dependent only for a brief period of its early life upon the small and insignificant gamobium. Thus while the gamobium is the dominant phase in the life-history of mosses, the agamobium appearing like a mere organ, in ferns the positions are more than reversed—the agamobium may assume the proportions of a tree, while the gamobium is so

small that its very existence is unknown to a large proportion of fern-collectors.

It follows from what has just been said that the various organs of a fern do not severally correspond with those of a moss. The leaves of a moss are not homologous with those of a fern, but are rather comparable to lobes of the prothallus: in the same way the rhizoids of a moss correspond, not with the complicated roots of the fern, but with the rhizoids of the prothallus.

LESSON XXXII

THE CHIEF DIVISIONS OF THE VEGETABLE KINGDOM: EQUISETUM: SALVINIA: SELAGINELLA

In the XXVIth Lesson (p. 304) it was pointed out that a thorough comprehension of the structure and development of Polygordius would enable the student to understand the main features of the organisation of all the higher animals.

In the same way the study of the fern paves the way to that of the higher groups of plants, all of which, indeed, differ far less from the fern than do the various animal forms considered in Lessons XXVI—XXIX from Polygordius. We saw that the differences between these included matters of such importance as the presence or absence of segmentation and of lateral appendages, the characters of the skeleton, and the structure and position of the nervous system. In the higher plants, on the other hand, the essential organs—root, stem, and leaves—are, save in details of form, size, &c., practically the same in all: the tissues always consist of epidermis, ground-parenchyma, and vascular bundles, the latter being divisible into phloëm and xylem: the growing point both of stem and of root is formed of meristem, from which the permanent tissues arise; and the growing point of

the root is always protected by a root-cap, that of the stem being simply over-arched by leaves. Moreover, an alternation of generations can be traced in all cases.

Plants may be conveniently divided into the following chief groups or phyla :

1. *Algæ.*
2. *Fungi.*
3. *Muscineæ.*
4. *Vascular Cryptogams.*
    a. Filicinæ.
    b. Equisetaceæ.
    c. Lycopodineæ.
5. *Phanerogams.*
    a. Gymnosperms.
    b. Angiosperms.

The *Algæ* are the lower green plants. They may be unicellular, or may take the form of linear, superficial, or solid aggregates: they never exhibit more than a limited amount of cell-differentiation. This group has been represented in the foregoing pages by Zooxanthella, Diatoms, Vaucheria, Caulerpa, Monostroma, Ulva, and Nitella.

The *Fungi* are the lower plants devoid of chlorophyll: some are unicellular, others are linear aggregates: in none is there any cell-differentiation worth mentioning. Saccharomyces, Mucor, Penicillium, and the mushroom belong to this group.

The position of some of the lower forms which have come under our notice is still doubtful. Bacteria, for instance, are considered by some authors to be Fungi, by others Algæ, while others place them in a group apart. Diatoms also are

sometimes placed in a distinct group. It must, moreover, be remembered that most botanists include Hæmatococcus, Pandorina, and Volvox among Algæ, and place the Mycetozoa either among Fungi or in a separate group of chlorophyll-less plants (p. 181).

The *Muscineæ* are the mosses and liverworts, the former of which were fully described in Lesson XXX.

The *Vascular Cryptogams* are flowerless plants in which vascular bundles are present. Together with the Phanerogams they constitute what are known as vascular plants, in contradistinction to the non-vascular Algæ, Fungi, and Muscineæ, in which no formation of vessels takes place. The group contains three subdivisions.

The first division of Vascular Cryptogams, the *Filicinæ*, includes the ferns, an account of which has been given in the previous lesson. It will be necessary, however, to devote some attention to an aquatic form, called *Salvinia*, which differs in certain important particulars from the more familiar members of the group.

The *Equisetaceæ* include the common horsetails (genus *Equisetum*), a brief account of which will be given, as they form an interesting link in their reproductive processes between the ordinary ferns and Salvinia.

The *Lycopodineæ*, or club-mosses, are the highest of the Cryptogams or flowerless plants. A short description of one of them, the genus *Selaginella*, will illustrate the most striking peculiarities of the group.

The *Phanerogams*, or flowering plants, are so called from the fact that their reproductive organs take the form of specially modified shoots, called cones or flowers. They are sometimes called by the more appropriate name of *Spermaphytes*, or seed-plants, from the fact that they alone among plants reproduce by means of seeds structures which differ

from spores in the fact that each contains an embryo plant in the phyllula stage.

The *Gymnosperms*, or naked-seeded Phanerogams, include the cone-bearing trees, such as pines, larches, cypresses, &c., as well as cycads and some other less familiar forms. A general account of this group will be given.

The *Angiosperms*, or covered-seeded Phanerogams, include all the ordinary flowering plants, as well as such trees as oaks, elms, poplars, chestnuts, &c. A brief description of the general features of this group will conclude the Lessons.

EQUISETUM

The horsetails are common British plants found usually in moist or marshy situations, and reaching a height of 1 to 3 feet.

The plant consists of a branched underground stem or rhizome, lateral branches of which grow vertically upwards, and constitute the *aërial shoots*. Both stem and branches have a very characteristic appearance: they are distinctly segmented or divided into nodes and internodes, and from each node springs a crown-like structure or *leaf-sheath* (Fig. 112, A, and Fig. 113, A, *l. sh*), formed by a whorl of leaves united into a continuous structure. In some cases the aërial shoots also give rise to secondary shoots (Fig. 112, A, *sh*), arranged in whorls and apparently arising below the leaves: actually, however, they originate in axillary buds, as in Nitella, but, instead of growing out between the stem and the leaf, perforate the base of the latter.

The internodes of both rhizome and aërial shoots are hollow, each having a large axial air-cavity (Fig. 112, B, c^1) extending throughout its whole length, and formed by the disintegration of the central parenchyma-cells of the young

stem. At each node is a transverse partition separating the internodal spaces from one another. Around the central cavity, and corresponding with the longitudinal ribs with which the stem is marked, is a series of smaller air-cavities (c^2), arranged in a circle, and alternating with these, between

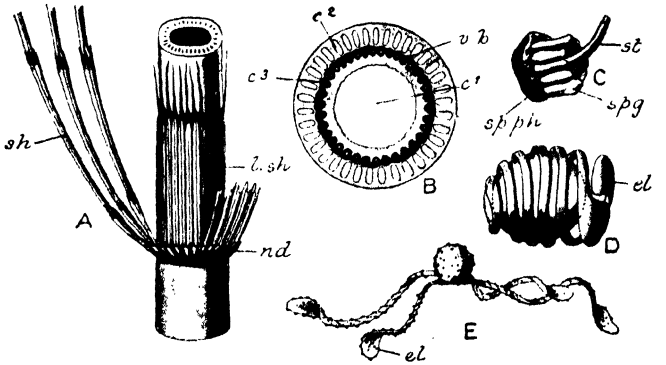

FIG. 112.—A, portion of aërial shoot of Equisetum, showing a node (*nd*) from which arise a leaf-sheath (*l. sh*) and a whorl of secondary shoots (*sh*). (Nat. size.)

B, transverse section of aërial shoot, showing central (c^1) and peripheral (c^2) air-cavities, and ring of vascular bundles with smaller air-cavities (c^3). (× 2.)

C, a single sporophyll (*sp. ph*) with stalk (*st*) and sporangia (*spg*). (× 10.)

D, a single spore showing coiled elater (*el*).

E, the same, with elater (*el*) expanded.

(A–C, after Goebel ; D and E, after Le Maout and Decaisne.)

them and the central cavity, are the vascular bundles (*v. b*), each with a small air-cavity (c^3) in its inner or central portion.

The microscopic structure of the plant agrees in essential respects with that of the fern, though differing in many details to which no further reference need be made here.

Each axis—rhizome and shoots—terminates in a tetrahedral apical cell.

As in ferns, there is no primary root in the adult, but numerous roots spring from the nodes of the rhizome, and agree in all essential points of structure and development with those of ferns.

Some of the aërial shoots bear only leaf-sheaths and branches, and are hence called *sterile shoots*: others, the *fertile shoots*, terminate in a cone-like structure (Fig. 113, A), formed of hexagonal scales (*sp. ph*), at first closely applied to one another at their edges, but afterwards becoming separated. Each scale (Fig. 112, C, and Fig. 113, B, *sp. ph*) is a mushroom-like body, springing from the axis of the cone by a stalk (*st*) attached to the centre of the inner surface of its expanded portion. Around the point of attachment of the stalk spring from five to ten elongated sacs, the *sporangia* (*spg*).

The structure and development of these mushroom-like bodies or scales of the cone show them to be peculiarly modified leaves, developed in whorls like the ordinary leaves of the stem, but not cohering into sheaths, and assuming the characteristic form just described in relation with their special function of bearing the sporangia. We have therefore to distinguish, in Equisetum, between ordinary or *foliage-leaves* and spore-bearing leaves or *sporophylls*.

The spores are developed in the same way as in mosses and ferns, but have a very distinctive structure. Outside the usual double cell-wall is a third coat, which, as development proceeds, becomes split up into four bands (Fig. 112, D, E, *el*), wound spirally round the spore and attached to it by one end, the opposite expanded end being free. These bands or *elaters* are hygroscopic: when moist they are coiled round the spore (D), when dry they straighten themselves

and stand out separately from its surface (E). The spores become entangled by their elaters, by the coiling and uncoiling of which they are able to execute slight movements.

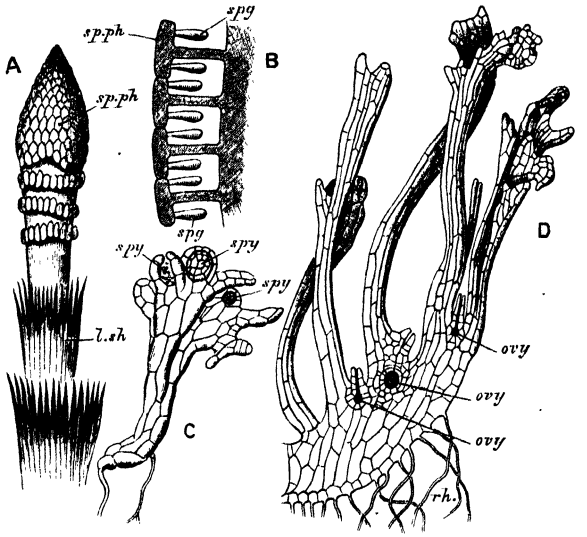

FIG. 113.—Reproduction and Development of *Equisetum*.

A, distal end of a fertile shoot, showing two leaf-sheaths (*l. sh*), and the cone formed of hexagonal sporophylls (*sp. ph*). (Nat. size.)

B, diagrammatic vertical section of a portion of the cone, showing the sporophylls (*sp. ph*) attached by short stalks to the axis of the cone, and bearing sporangia (*spg*) on their inner surfaces.

C, a male prothallus bearing three spermaries (*spy*). (× 100.)

D, portion of a female prothallus bearing three ovaries (*ovy*), those to the right and left containing ova, that in the middle a polyplast; *rh*, rhizoids. (× 30.)

(A, after Le Maout and Decaisne; C and D, after Hofmeister.)

The spores are liberated by the bursting of the sporangia, and germinate, giving rise to prothalli. But instead of the prothalli being all alike in form and size and all monœcious,

some (c) remain small and simple, and produce only spermaries (*spy*); others (D) attain a complicated form and a length of over a centimetre, and produce only ovaries (*ovy*). Thus although there is no difference in the spores, the prothalli produced from them are of two distinct kinds, the smaller being usually exclusively male, the larger female.

The oosperm develops in much the same way as in ferns: it divides and forms a polyplast, which, by formation of a stem, root, foot, and two cotyledons, becomes a phyllula and grows into the adult plant.

As in the fern, the Equisetum plant, reproducing as it does by asexual spores, is the agamobium, the gamobium being represented by the prothallus. The peculiarity in the present case is that the gamobium is sexually dimorphic, some prothalli producing only male, others only female gonads.

SALVINIA

Salvinia is a small fresh-water plant, found floating, like duckweed, on the surface of still water.

The stem (Fig. 114, *st*) is an elongated slender rhizome floating at or near the surface, and distinctly divided into nodes and internodes. Each node gives off three appendages, two broad, flat foliage-leaves (*f. l.* 1–3; *f. l.* 1′–3′), which lie above the surface of the water, and a branched structure (*s. l.* 1–3) which has all the appearance of a root, its thread-like branches hanging down into the water and being covered with hairs. The study of their development shows, however, that these organs arise exogenously from the node and have no root-cap: they are, in fact, not roots, but *submerged leaves*, performing the function of roots.

The latter organs are, quite exceptionally among the higher plants, wholly absent.

The stem ends distally in a terminal bud (*t. bd*), the

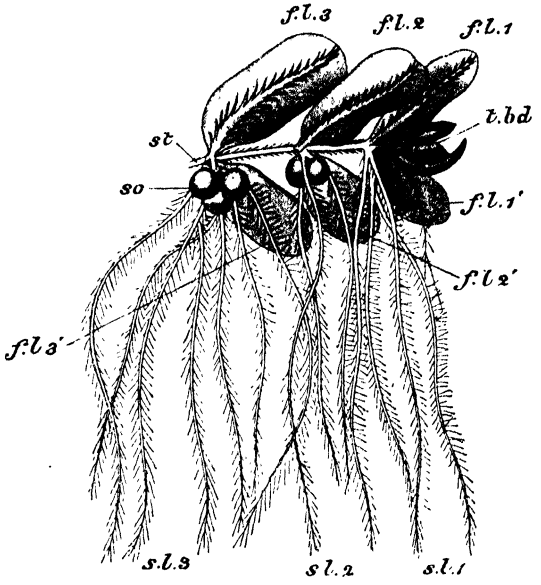

FIG. 114.—Distal portion of a Salvinia plant seen obliquely from below.

The stem (*st*) ends in a terminal bud (*t. bd*), and the part figured contains three nodes, each bearing a pair of foliage-leaves (*f. l.* 1–3, *f. l.* 1′–3′), and a much-divided root-like submerged leaf (*s. l.* 1–3). On the bases of the submerged leaves are borne groups of sori (*so*), containing sporangia. (Slightly enlarged.)

(From Vines, after Sachs.)

growing point of which is formed by a two-sided apical cell: it is traversed by a single vascular bundle, which sends branches into the leaves.

Springing from the bases of the submerged leaves are numerous globular capsules (*so*), each containing a number of sporangia. The wall of the capsule (Fig. 115, A) corresponds with the indusium of a fern, and the contained group of sporangia with a sorus. But the sori of Salvinia, unlike those of ordinary ferns, are dimorphic, some containing a comparatively small number of large sporangia (*mg. spg*), others a much larger number of small ones (*mi. spg*). The larger kind, distinguished as *megasporangia*, contain each a single large spore, or *megaspore:* the smaller kind, or *microsporangia*, contain a large number of minute spores, like those of an ordinary fern, and called *microspores*. It is this striking dimorphism of the sori, sporangia, and spores which forms the chief distinction between Salvinia and its allies and the true ferns.

When ripe the sporangia become detached and float on the surface of the water. The microspores germinate (B), while still enclosed in their sporangium: each sends out a filament, which protrudes through the wall of the microsporangium, its extremity (*spy*) becoming separated off by a septum and then divided into two cells. The protoplasm of each of these divides into four sperm-mother-cells, and from these spirally-twisted sperms are produced in the usual manner. It is obvious that the two cells in which the sperms are developed represent greatly simplified spermaries: the single proximal cell (*prth*) of the filament arising from the microspore, a still more simplified prothallus. Both prothallus and spermaries are vestigial structures; the prothallus is microscopic and unicellular instead of being a solid aggregate of considerable size, as in the two preceding types; each spermary forms only four sperm-mother-cells, and the total number of sperms is therefore reduced to eight.

The contents of the megaspore are divisible into a comparatively small mass of protoplasm at one end, and of starch grains, oil-globules, and proteid bodies, which fill up the rest

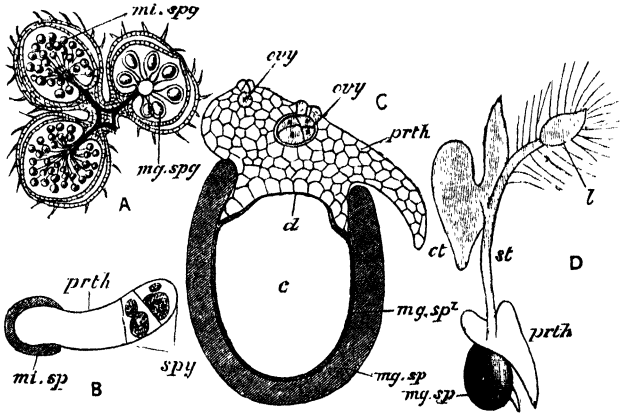

FIG. 115 —Reproduction and Development of *Salvinia.*

A, portion of a submerged leaf, showing three sori in vertical section, two containing microsporangia (*mi. spg*) and one megasporangia (*mg. spg*). (× 10.)

B, a germinating microspore (*mi. spg*), showing the vestigial prothallus (*prth*) and its two spermaries (*spy*). (× 150.)

C, diagrammatic vertical section of a germinating megaspore, showing the outer (*mg. sp*) and inner (*mg. sp*¹) coats of the spore, and its cavity (*c*) containing plastic products, separated by a septum (*d*) from the prothallus (*prth*), in which two ovaries (*ovy*) are shown, that to the left containing an ovum, that to the right a polyplast. (× 50.)

D, megaspore (*mg. sp*) with prothallus (*prth*) and phyllula just beginning to develop into the leafy plant : *st*, stem ; *ct*, cotyledon ; and *l*, outermost leaf of the terminal bud. (× 20.)

(A and B, after Sachs ; D, after Pringsheim.)

(C, *c*) of the spore. The megaspore has, in fact, attained its large size by the accumulation of great quantities of plastic products, which serve as nutriment to the future prothallus

and embryo, after the manner of the yolk in the eggs of the crayfish and dogfish.

The protoplasm of the megaspore (c) divides and forms a prothallus (*prth*) in the form of a three-sided multicellular mass projecting from the spore, which it slightly exceeds in size. Three ovaries (*ovy*) are formed on it, having much the same structure as in ordinary ferns: if neither of these should be fertilised others are developed subsequently. Thus the reduction of the prothallus produced from the megaspore, although obvious, is far less than in the case of that arising from the microspore.

We see that sexual dimorphism has gone a step further in Salvinia than in Equisetum: not only are the prothalli differentiated into male and female, but also the spores from which they arise.

Impregnation takes place in the usual way, and the oosperm divides to form a polyplast, which, by differentiation of a stem-rudiment, a cotyledon, and a foot, passes into the phyllula stage: no root is developed in Salvinia. By the gradual elongation of the stem (D, *st*) and the successive formation of whorls of leaves (*l*), the adult form is assumed.

Thus the life-history of Salvinia resembles that of the fern, but with two important differences: the spores are dimorphic, and the gamobium, represented by the male and female prothalli, is greatly reduced.

SELAGINELLA

Selaginella, one of the club-mosses, is common on hill-sides in many parts of the world. In the commoner species there is a creeping stem which forks repeatedly in the horizontal plane, and bears numerous small, close-set leaves, giving the whole plant much the appearance of a moss.

The leaves (Fig. 116, A) arise in four longitudinal rows, but, owing to the horizontal position of the plant, the two rows belonging to the lower side (l^2) project laterally, and

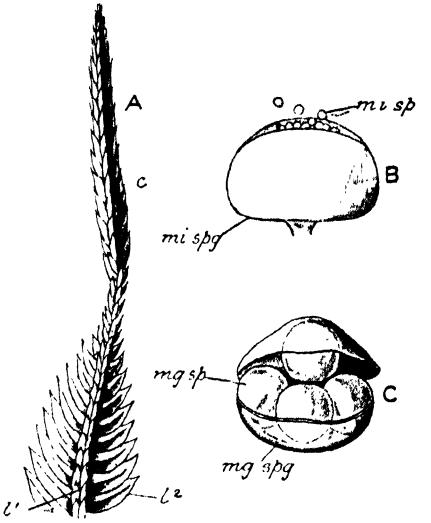

FIG. 116.—A, distal end of a shoot of Selaginella, showing the two rows of small dorsal leaves (l^1), the two laterally placed rows of ventral leaves (l^2), and the terminal cone (c). (Nat. size.)

B, a microsporangium bursting to allow of the escape of the microspores (*mi. sp*).

C, a megasporangium, with four megaspores (*mg. sp*).

(A, after Sachs ; B and C, after Le Maout and Decaisne.)

are many times larger than the two upper rows (l^1). Each leaf bears on its upper or distal surface, near the base, a small process called a *ligule*.

The stem usually ends in a two- or three-sided apical cell, from which segments are cut off to form the apical

meristem, but in some species no apical cell can be distinguished. There are from one to three vascular bundles running through the stem, each surrounded by a ring of small air-cavities: from them a single bundle is given off to each leaf. The presence of vascular bundles and of a well-marked epidermis is enough to distinguish our present type from the mosses, to which it bears a superficial resemblance.

The peculiar forked branching is due to the development of lateral branches alternately on each side of the stem. The roots arise from peculiar leafless branches, sometimes mistaken for true roots.

The branches terminate in cones (Fig. 116, A, C, and Fig. 117, A) formed of small leaves (*sp. ph*), which overlap in somewhat the same way as the scales of a pine-cone. Each of these leaves is a sporophyll, and bears on its upper or distal side, near the base, a globular sporangium. The sporangia are fairly uniform in size, but some are megasporangia (Fig. 116, C, and Fig. 117, A, *mg. spg*), and contain usually four megaspores; others are microsporangia (Fig. 116, B, and Fig. 117, A, *mi. spg*), containing numerous microspores.

The microspore (Fig. 117, B) cannot be said to germinate at all. Its protoplasm divides, forming a small cell (*prth*), which represents a vestigial prothallus, and a large cell, the representative of a spermary. The latter (*spy*) undergoes further division, forming six to eight cells in which numerous sperm-mother-cells are developed. The sperms are finally liberated by the rupture of the coats of the microspore.

A similar but less complete reduction of the prothallus is seen in the case of the megaspore (C). Its contents are divided, as in Salvinia, into a small mass of protoplasm at one end; and a large quantity of plastic products filling up the rest of its cavity. The protoplasm divides and forms a small prothallus (*prth*), and a process of division also takes

place in the remaining contents (*prth*^{1}) of the spore, producing a large-celled tissue, the *secondary prothallus*.

By the rupture of the double cell-wall of the megaspore

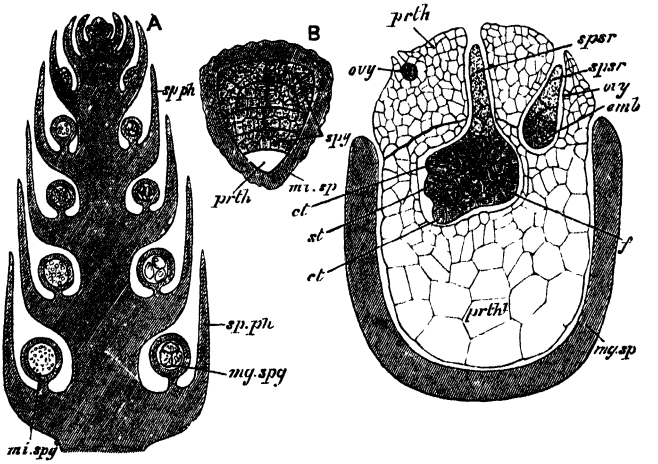

FIG. 117.—Reproduction and Development of *Selaginella*.

A, diagrammatic vertical section of a cone, consisting of an axis bearing close-set sporophylls (*sp. ph*), on the bases of which microsporangia (*mi. spg*) and megasporangia (*mg. spg*) are borne.

B, section of a microspore, showing the outer coat (*mi. sp*), prothallial cell (*prth*), and multicellular spermary (*spy*).

C, vertical section of a megaspore, the wall of which (*mg. sp*) has been burst by the growth of the prothallus (*prth*): its cavity (*prth*^{1}) contains a large-celled tissue, the secondary prothallus: in the prothallus are three ovaries (*ovy*), that to the left containing an ovum, that to the right an embryo (*emb*) in the polyplast stage, and that in the centre an embryo in the phyllula stage, showing stem-rudiment (*st*), foot (*f*), and two cotyledons (*ct*): both embryos are provided with suspensors (dotted) (*spsr*), and have sunk into the secondary prothallus.

(Altered from Sachs.)

the prothallus is exposed to the air, but it never protrudes through the opening thus made, and is, therefore, like the corresponding male structure, purely endogenous. One or

more ovaries (*ovy*) are formed on it, each consisting of a short neck, an ovum, and two canal-cells afterwards converted into mucilage: there is no venter, and the neck consists of only two tiers of cells.

The oosperm divides by a plane at right angles to the neck of the ovary, forming the earliest or two-celled stage of the polyplast. The upper cell undergoes further division, forming an elongated structure, the *suspensor* (*spsr*): the lower or embryo proper (*emb*) is forced downwards into the secondary prothallus by the elongation of the suspensor, and soon passes into the phyllula stage by the differentiation of a stem-rudiment (*st*), two cotyledons (*ct*), a foot (*f*), and subsequently of a root.

A further reduction of the gamobium is seen in Selaginella: both male and female prothalli are quite vestigial, never emerging from the spores: and the spermary and ovary are greatly simplified in structure.

LESSON XXXIII

GYMNOSPERMS

THE commonest Gymnosperms are the evergreen cone-bearing trees such as pines, spruces, larches, cypresses, and yews. They all have a primary axis or *trunk* from which branches arise in a monopodial manner, *i.e.*, the oldest are near the proximal, the youngest near the distal end. The branches give off, in successive seasons, branches of a higher order, so that the older or lower branches are always themselves more or less extensively ramified, and the whole plant tends to assume a conical form, the base of the cone being formed by the oldest secondary axes springing from the base of the trunk, the apex by the distal end of the primary axis.

The branches are all axillary, each arising from the axil of a leaf, and, like the main stem, ending distally in a terminal bud. The foliage-leaves differ greatly in the various genera of Gymnosperms: in the pines they are long, needle-like structures, borne in pairs on short axillary branches or dwarf-shoots.

In correspondence with the size attained by the aërial portion of the plant, the root attains far greater relative dimensions than in any case we have previously studied.

The trunk is continued downwards by a great *primary root*, from which secondary roots arise in regular order, and, these branching again and again, there is produced a root-system of immense size and complexity, extending into the soil to a sufficient depth to resist the strain to which the aërial part of the tree is subjected by the wind.

One remarkable feature about the pines and their allies as compared with the plants previously studied, is their practically unlimited growth. In mosses, ferns, &c., the stem after attaining a certain diameter ceases to grow in thickness, so that even in the tallest tree-ferns the stem is always slender. But in pines the trunk, the branches, and the roots continue to increase in thickness for an indefinite period, the trunk in the common Scotch Fir (*Pinus sylvestris*) attaining a circumference of four or five metres or even more, and the other parts in proportion. The tree may survive for hundreds of years.

The changes undergone during this remarkable process of growth are best studied, in the first instance, by a series of rough transverse sections of branches of different ages. In a first year's branch the middle is occupied by an axial strand of soft tissue, the *pith* or *medulla* (Fig. 118, A and B, *med*); outside this comes a ring of *wood* (*xy*), divided into radially arranged wedge-shaped masses; and this in turn is surrounded by the *bark* or *cortex* (*cor*), which can be readily stripped off the wood, and which contains numerous *resin-canals* (*r. c*) appearing in the section as rounded apertures with drops of resin oozing from them. In a somewhat older branch the layer of wood is seen to have increased greatly in thickness, and has a well-marked concentric and radial striation (C): the cortex also has thickened though to a less extent, while the pith is unaltered. The bark, moreover, is clearly divisible into an inner light coloured layer, the *bast*

or *phlöem* (*phl*), a middle green layer of *cortical parenchyma* (*cor*) containing resin-canals, and an outer brown layer, the *cork* (*ck*). Lastly, in the trunk and larger branches the wood forms by far the greater part of the whole section, the bark being a comparatively thin layer, easily stripped off, with no

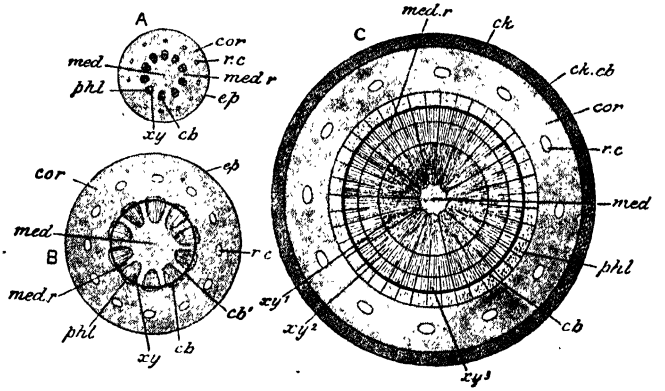

FIG. 118.—Diagrammatic transverse sections of three branches of *Pinus* of different ages.

A, very young axis, showing epidermis (*ep*), cortex (*cor*) with resin-canals (*r. c*), medulla (*med*), and ring of vascular bundles, separated by medullary rays (*med. r*), and each consisting of xylem (*xy*), cambium (*cb*), and phlöem (*phl*).

B, older axis, in which the cambium forms a complete cylinder, owing to the formation of interfascicular cambium (*cb'*) between the bundles.

C, Axis of the third year, showing xylem of first (xy^1), second (xy^2), and third (xy^3) year's growth; cork (*ck*); and cork-cambium (*ck. cb.*)

cortical parenchyma, and with its corky outer layer much thickened, gnarled, and wrinkled.

The wood has been stated to exhibit both concentric and radial striations. The radial markings are called *medullary rays* (Fig. 118, C, *med. r*) and follow the "grain" of the

wood. The concentric markings, which are against the grain, are the *annual rings* (xy^1, xy^2, xy^3), and owe their existence to the fact that the wood formed in summer and autumn is denser than that formed in spring, while in winter there is a cessation of wood-production. Thus, by counting the annual rings of the main trunk, the age of the tree may be estimated. The wood, it will be observed, grows from within outwards, a new layer being added each year outside the old.

The power of indefinite increase in diameter, which is so striking a feature in the pines and their allies, is connected with a peculiarity in the structure and arrangement of the vascular bundles. In the very young condition, *i.e.*, in the terminal bud, the vascular bundles of the stem (Fig. 118, A) are wedge-shaped in transverse section and are arranged in a circle, the apex of each being turned towards the axis of the stem, the base towards its periphery. Actually, of course, as in the fern, the bundles are longitudinal strands with prolongation into the leaves.

The arrangement of the tissues in the vascular bundles differs in an important respect from the condition we are familiar with in the fern. Instead of the xylem occupying the centre of the bundle and being surrounded by phlöem, the xylem (Fig. 118, A, *xy*) forms the whole of the in-turned side, *i.e.*, the narrow portion of the wedge in transverse sections, the phlöem (*phl*) the outer portion or broad end of the wedge. In a word, the bundles are not *concentric* as in the fern, but *collateral*. Moreover, the phlöem and xylem are separated by a layer of small thin-walled cells, called the *cambium* layer (*cb*).

By this arrangement of the vascular bundles the ground-parenchyma of the stem is divisible into three portions, an external layer, the *cortex* (*cor*), between the epidermis (*ep*),

and the phlöem bundles, an axial cylinder, the *pith* or *medulla* (*med*), internal to the xylem bundles, and a series of radial plates, the *primary medullary rays* (*med. r*) separating the bundles from one another.

As development proceeds the parenchyma-cells connecting the cambium of adjacent bundles take on the characters of cambium-cells, the result being the formation of a closed cambium-cylinder, or, in transverse section, cambium-ring (B, *cb*, *cb'*). In this a distinction is to be drawn between the *fascicular cambium* (*cb*) or original cambium of the bundles and *inter-fascicular cambium* (*cb'*) formed by conversion of cells of the medullary rays.

The cambium-cells now begin to divide in a tangential direction, *i.e.*, along a plane parallel to the surface of the stem. If this process went on alone the result would be simply an increase in the thickness of the cambium layer, but as it proceeds the products of division of the cells on the inner face of the cambium-cylinder become converted into new xylem-elements, those on its outer face into new phlöem-elements. We have thus a formation of *secondary wood* and *secondary bast*, which, being formed from the whole of the cambium-cylinder, show no division into bundles but form a continuous cylinder (C, *xy*, *phl*) of constantly increasing thickness. The phlöem now forms the inner layer of the bark, which, as we have seen, can be readily stripped from the wood owing to the delicate cambium-cells being easily torn apart.

At the same time a layer of cells of the cortical parenchyma begins to divide tangentially so as to form a cylinder, or in transverse section a ring, of *cork-cambium* (Fig. 118, C, *ck. cb*), from the outer face of which layer after layer of cork-cells (*ck*) is formed. In the cork-cells the protoplasm disappears and the cell-walls undergo a peculiar change by

which they become waterproof: this process, besides protecting the interior of the stem from external moisture, prevents the access of nutrient matters to the epidermis and outer layers of cortical parenchyma. Both these layers consequently die and peel off, the outer surface coming to be formed by the cork itself.

The wood of pines contains no vessels, *i.e.*, cells joined end to end so as to form a continuous tube, but only tracheides, *i.e.*, elongated spindle-shaped cells with lignified walls and devoid of protoplasm (p. 417). Radial bands of cells mostly parenchymatous, are formed between the tracheides of the secondary wood, and give rise to the *secondary medullary rays* (c, *med. r*) to which the radial striation of the wood is due: they increase in number with the increase in thickness of the wood. The tracheides formed in autumn have smaller cavities and thicker walls than those formed in spring and summer: hence the formation of annual rings. The tracheides are not scalariform like those of ferns, but their walls have at intervals circular depressions perforated in the centre and called *bordered pits*. The tracheides of the primary xylem bundles have spirally thickened walls, like the spiral vessels of ferns. The phlöem, both primary and secondary, consists of sieve-tubes and parenchyma.

The growing point of Gymnosperms presents a striking difference to that of ferns and other flowerless plants. It consists simply of a mass of meristem cells among which no apical cell is to be distinguished.

Pines, like horsetails and club-mosses, reproduce by means of *cones* or *flowers*. These are of two kinds, male and female, so that sexual differentiation is carried a step further than in Selaginella, in which sporangia of both sexes

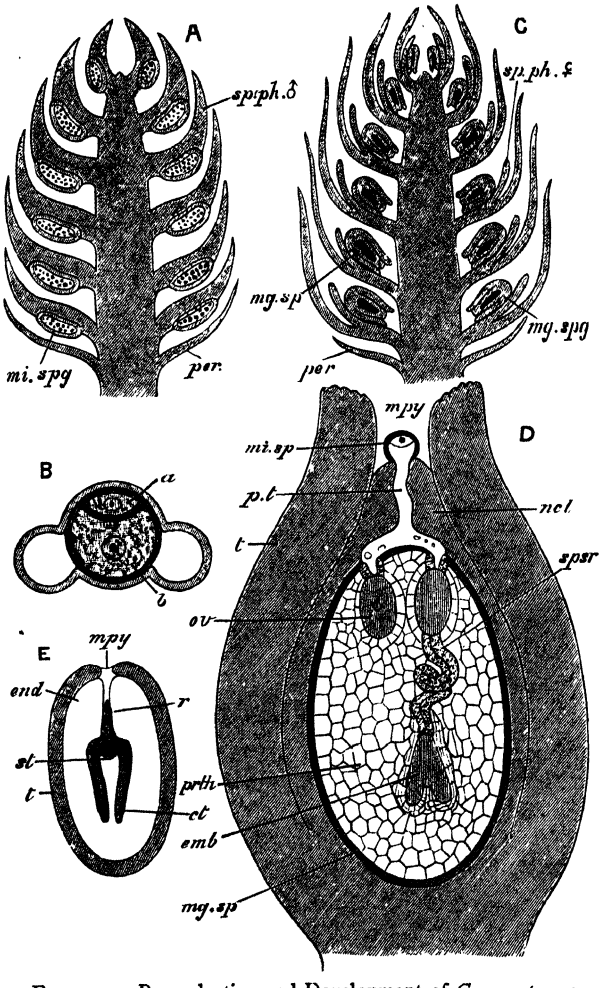

FIG. 119.—Reproduction and Development of *Gymnosperms*.
A, diagrammatic vertical section of male cone, showing axis with male sporophylls (*sp. ph.* ♂) bearing microsporangia (*mi. spg*): *per*, scale-like leaves forming a rudimentary perianth.

B, a single microspore, showing bladder-like processes of outer coat, and contents divided into small prothallial cell (*a*) and large cell (*b*), from which the pollen-tube arises.

C, diagrammatic vertical section of female cone, showing axis with female sporophylls (*sp. ph.* ♀) bearing megasporangia (*mg. spg*), each of which contains a single megaspore (*mg. sp*) : *per*, the scale-like perianth leaves.

D, diagrammatic vertical section of a megasporangium, showing cellular coat (*t*), and nucellus (*nct*), micropyle (*mpy*), and megaspore (*mg. sp*) : the latter contains the prothallus (*prth*) in which are two ovaries, that to the left showing a large ovum (*ov*) and neck-cells, while that to the right has given rise to an embryo (*emb*) which is in the phyllula stage, and has sunk into the tissue of the prothallus by the elongation of the long suspensor (*spsr*).

A microspore (*mi. sp*) is seen in the micropyle sending off a pollen-tube (*p. t*), the end of which is applied to the necks of the two ovaries.

E, diagrammatic vertical section of a seed, showing coat (*t*), micropyle (*mpy*), and endosperm (*end*), in which is imbedded an embryo in the phyllula stage, consisting of stem-rudiment (*st*), cotyledons (*ct*), and root (*r*).

(A and B, altered from Strasburger ; D and E, altered from Sachs.)

are borne on the same cone. In the pines and their allies both male and female cones are usually borne on the same tree, so that the plant is *monœcious:* many Gymnosperms, on the other hand, are *diœcious*, each tree bearing either male or female cones only.

The male cones (Fig. 119, A) are borne in clusters or *inflorescences* near the distal ends of the branches. Each cone consists, as in Equisetum and Selaginella, of an axis bearing a large number of sporophylls (*sp. ph.* ♂) : it springs from the axil of a leaf and is to be looked upon as an abbreviated and peculiarly modified shoot.

The sporophylls or *stamens* as they are commonly called (Figs. 119, *sp. ph.* ♂ and Fig. 120), are more or less leaf-like structures, each consisting of a short stalk or *filament* and an expanded portion or *anther*, the latter bearing on its under or proximal side two microsporangia or pollen-sacs (*mi. spg*). The mother-cells of these divide each into four microspores or *pollen-grains*, which are liberated by the rupture of the

microsporangia in immense quantities, in the form of clouds of light yellow powder called *pollen*. The microspore (B) is at first an ordinary cell consisting of protoplasm with a nucleus and a double cell-wall, but eventually the protoplasm divides into two cells; a small one (*a*), the vestige of the male prothallus, which soon divides again forming two or more cells, one of which is distinguished as the *generative cell*; and a large one (*b*), the *vegetative cell*. Under favourable circumstances these cells undergo changes which will be described presently.

The structure of the female cone is best made out in the

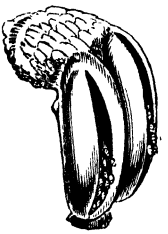

FIG. 120.— A single stamen or male sporophyll of the pine, showing the two microsporangia or pollen-sacs.

larch. It also consists (Fig. 119, C) of an axis bearing sporophylls (*sp. ph.* ♀), or, as they are usually called in Phanerogams, *carpels*. Each carpel is a crimson leaf with a green midrib produced distally into a projecting point, and bears on its upper or distal surface a little flattened body, the *placental scale*, on the upper surface of which are two peculiarly modified megasporangia (*mg. spg.*), commonly known as *ovules*. In the pine the placental scales (Fig. 121) are larger than the carpels, and their thickened distal ends form the rhomboid areas into which the surface of the cone is divided.

The comparison of the reproductive organs of the pine and larch with those of Vascular Cryptogams and of Angiosperms will be facilitated by a consideration of two exotic genera of palm-like Gymnosperms. In *Zamia* both male (Fig. 122, A) and female (B) cones bear a close external resemblance to those of Equisetum, the sporophylls (*sp. ph.* ♂, *sp. ph.* ♀) being stalked hexagonal scales on the inner surfaces of which the pollen-sacs (B, *mi. spg*) or ovules (D, *mg. spg*) are borne. In the female *Cycas* the carpels (E, *sp. ph.* ♀) are not arranged in a cone, but form a whorl

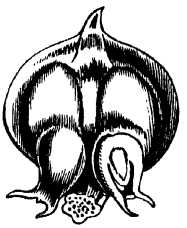

FIG. 121.—A single carpel or female sporophyll of pine, with placental scale bearing two megasporangia or ovules.

of leaf-like bodies obviously homologous with foliage leaves. Each carpel is, in fact, a leaf 20–30 cm. long, and deeply lobed at its edge: in the distal portion the lobes are long and slender, but proximally they take the form of ovoidal bodies (*mg. spg*), about the size of plums, the ovules or megasporangia.

The ovules differ strikingly in structure from the megasporangia of Cryptogams. Each consists of a solid mass of small cells called the *nucellus* (Fig. 119, D, *ncl*), attached by its proximal end to the sporophyll, and surrounded by a wall or *integument* (*t*) also formed of a small-celled tissue. The

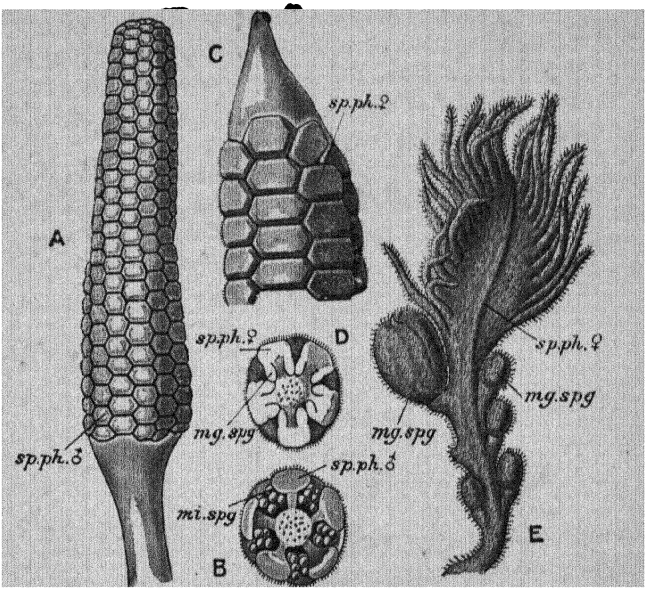

FIG. 122.—A, male cone of *Zamia*, showing the hexagonal sporophylls (*sp. ph.* ♂).

B, transverse section of the same, showing the microsporangia (*mi. spg*) borne on the sporophylls.

C, distal end of female cone of *Zamia*, showing the sporophylls (*sp. ph.* ♀).

D, transverse section of the same, showing the megasporangia (*mg. spg*) borne on the sporophylls.

E, a single female sporophyll (*sp. ph.* ♀) of Cycas, the pointed lobes of the distal portion replaced proximally by megasporangia (*mg. spg*). (After Sachs.)

integument is in close contact with the nucellus, but is perforated distally by an aperture, the *micropyle* (*mpy*), through which a small area of the nucellus is exposed.

Each megasporangium contains only a single megaspore,

frequently called the *embryo sac* (C and D, *mg. sp*), and having the form of a large ovoidal body embedded in the tissue of the nucellus. It has at first the characters of a single cell, but afterwards, by division of its nucleus and protoplasm, becomes filled with small cells representing a prothallus (*prth*). As in Vascular Cryptogams, single superficial cells of the prothallus are converted into ovaries which are extremely simple in structure, each consisting of a large ovum (*ov*), and of a variable number of neck-cells.

The pollen, liberated by the rupture of the microsporangia, is carried to considerable distances by the wind, some of it falling on the female cones of the same or another tree. In this way single microspores (pollen-grains) find their way into the micropyle of a megasporangium (D, *mi. sp*). This is the process known as *pollination*, and is the necessary antecedent of fertilisation.

The microspore now germinates: the outer coat bursts, and the vegetative cell (B, *b*) protrudes in the form of a filament resembling a hypha of Mucor, and called a *pollen-tube* (D, *p.t*). This forces its way into the tissue of the nucellus, like a root making its way through the soil, and finally reaches the megaspore in the immediate neighbourhood of an ovary. A process then grows out from the end of the tube, passes between the neck-cells, and comes in contact with the ovum.

In the meantime the nucleus of the vegetative cell (*b*)—that from which the pollen-tube grows—has travelled towards the end of the pollen-tube and undergone degeneration. The generative cell at the same time enters the pollen-tube and divides into two *sperm-cells*. The end of the pollen-tube becomes mucilaginous and one of the sperm-cells makes its way through it, down the neck of the ovary and into the ovum. The nucleus of the sperm-cell—called the *male*

pronucleus—then conjugates with the nucleus of the ovum, or *female pronucleus*, and thus effects the process of fertilisation, or the conversion of the ovum into the oosperm.

The development of the oosperm is a very complicated process, and results in the formation not of a single polyplast but of four, each at the end of a long suspensor (D, *spsr*), formed of a linear aggregate of cells, which by its elongation carries the embryo (*emb*) down into the tissue of the prothallus. As a rule only one of these embryos comes to maturity: it develops a rudimentary stem, root, and four or more cotyledons, and so becomes a phyllula.

While these processes are going on the female cone increases greatly in size and becomes woody. The megasporangia, now called *seeds*, also become much larger, their integuments (E, *t*), becoming brown and hard and constituting the seed-coat or *testa*, which in the pine is produced into a flattened expansion or *wing*. The megaspore in each seed enlarges so much as to displace the nucellus: at the same time the cells of the prothallus filling the megaspore develop large quantities of plastic products, such as fat and albuminous substances, to be used in the nutrition of the embryo: the tissue thus formed is the *endosperm* (*end*).

As the cone dries the placental scales separate and expose the seeds, which drop out and may be carried considerable distances by the wind acting upon their wings, before falling to the ground.

Under favourable circumstances the seed germinates. By absorption of moisture its contents swell and burst the seed-coat, and the root of the phyllula (*r*) emerges, followed before long by the stem (*st*) and cotyledons (*ct*). The phyllula thus becomes the seedling plant, and by further growth and the successive formation of new parts is converted into the adult.

In Gymnosperms we see an even more striking reduction of the gamobium than in Selaginella. The female prothallus is permanently inclosed in the megaspore, and the megaspore in the megasporangium: the ovaries also are greatly simplified. The male prothallus is represented by the smaller cell of the microspore, and no formation of sperms takes place, fertilisation being effected by sperm-cells formed from one of the products of division of the prothallial cell, which migrate to the extremity of a tubular prolongation of the larger or vegetative cell of the microspore, and finally conjugate with the ova.

It is worthy of notice that in spite of the specialised method of fertilisation in Phanerogams, the process is essentially the same as in other organisms.

LESSON XXXIV

ANGIOSPERMS

To this group belong all the commoner herbs and shrubs as well as trees other than Gymnosperms, such as palms, oaks, elms, beeches, poplars, &c. There are two subdivisions of the group which must be mentioned, because of the necessity of referring to them later on: they are the *Dicotyledons*, so called because of the presence of two cotyledons or seed-leaves in the phyllula, and the *Monocotyledons*, in which only a single seed-leaf is present. Among Dicotyledons are included the large majority of wild and garden flowers, as well as most of the angiospermous trees: the best known Monocotyledons are the lilies and their allies, the various kinds of narcissus, orchids, grasses, and palms.

The general relations of the main parts of the plant—stem, root, leaves, &c.—are the same as in Gymnosperms, as may be seen by comparing a wallflower, an elm, a poplar, and a lily, taken as examples of dicotyledonous herbs, of dicotyledonous trees, and of Monocotyledons respectively. In the lily, however, as in Monocotyledons generally, there is no primary root, but a great number of equal-sized root-fibres springing from the base of the stem.

In Dicotyledons the arrangement of the tissues is the same as in Gymnosperms (p. 448): the vascular bundles

are arranged in a circle, and there is a closed cambium cylinder from which new xylem is added internally, and new phlöem externally. Moreover, in trees and shrubs, *i.e.*, plants which survive from year to year instead of dying down at the end of one or two seasons, a cork-cambium is formed

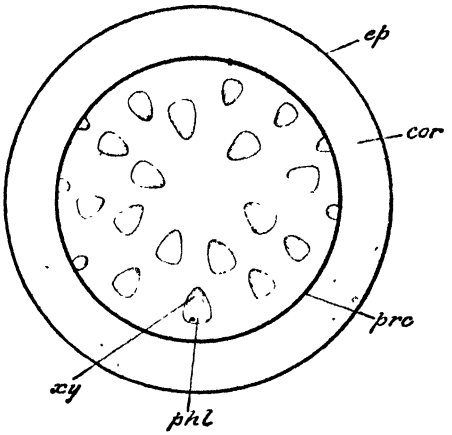

FIG. 123.—Diagrammatic transverse section of the stem of a Lily, showing the epidermis (*ep*), cortical parenchyma containing chlorophyll (*cor*), and axial cylinder of parenchyma surrounded by the pericycle (*prc*) and containing vascular bundles, each consisting of phloem (*phl*) and xylem (*xy*).

in the cortex from which an external layer of cork is produced, the epidermis disappearing. So that the phenomena of growth in thickness can be studied as conveniently in any dicotyledonous tree as in a pine or cypress.

In Monocotyledons—in a lily, for instance—the arrangement of tissues is different. The vascular bundles (Fig. 123) are arranged in a number of irregular circles scattered throughout the central parenchyma or ground tissue, which

is separated from the cortical parenchyma (*cort*) by a layer of sclerenchymatous cells, the *pericycle* (*prc*). The bundles are collateral, the xylem (*xy*) facing the axis of the stem, the phlöem (*phl*) its periphery: but there is a fundamental difference from the bundles of Gymnosperms and Dicotyledons in that the fully formed bundle contains no cambium, and is therefore incapable of further growth. The bundles of Monocotyledons are therefore *closed*, while those of Gymnosperms and Dicotyledons are *open*. Owing partly to this circumstance, partly to the thick unyielding pericycle, the stems of nearly all Monocotyledons are incapable, when once their tissues are fully formed, of further increase in thickness. Hence the characteristic slenderness of the trunk of a palm as compared with that of a pine or an oak.

The wood of Angiosperms consists of spiral, annular and dotted vessels, of fibres or prosenchymatous cells, and of parenchyma. The phlöem contains sieve-tubes, long tough prosenchymatous cells called bast-fibres, and parenchyma. The growing point, as in Gymnosperms, has no apical cell.

The leaves vary indefinitely in form, and all that can be mentioned with regard to them in the present brief sketch is that in most Monocotyledons they are long and narrow, and traversed by numerous parallel veins, while in Dicotyledons they are generally broad, with a smaller number—one to five—of primary veins from which secondary veins branch out and unite in a network. So that the *venation* or veining is *parallel* in Monocotyledons, *reticulate* in Dicotyledons.

It is in the structure of the flower that the most striking differences from, and the most marked advance upon,

Gymnosperms are seen. The modifications of the flower among both groups of Angiosperms are almost infinite, and can be thoroughly understood only by a careful study of numerous forms: all that can be attempted here is to give some idea of the essential points of structure and the leading modifications, by reference to a few selected forms.

In a buttercup (*Ranunculus*), one of the most generalised Dicotyledons, the flower is borne at the end of a long stalk or *peduncle* (Fig. 124, A and B, *pd*), the distal end of which is expanded into a conical *floral receptacle* (B and C, *fl. r*), serving for the attachment of the various parts of the flower.

From the broad proximal end of the receptacle spring five greenish leaves (A and B, *cp*), arranged in a whorl: they are the *sepals*, and together constitute the *calyx* of the flower. A little higher up arise, alternately with the sepals, five larger leaves (A and B, *pt*) of a brilliant yellow colour, forming the conspicuous part of the whole flower: they are the *petals*, and together constitute the *corolla*. Each petal has at the base of its upper side a little scale called a *nectary* (F, *nct*), from which a sweet juice, called *nectar*, is secreted.

Both sepals and petals spring from the base of the conical receptacle. From the lower half of the part above their origin arise a large number of *stamens* (B and C, *st*), arranged, not in a whorl, but in a close spiral, and together constituting the *andrœcium*. Each stamen (D) consists of a stalk or filament (*fl*), bearing at its distal end an expanded body or *anther* (*an*), divided by longitudinal ridges into four lobes. A transverse section (Fig. 125, B^2) shows that each lobe contains a pollen-sac or microsporangium (*mi. spg*), filled, in the ripe condition, with minute pollen-grains or microspores (*mi. sp*).

From the distal portion of the receptacle arise, also in a close spiral, a number of little pod-like bodies, the *carpels*

(B and C, *cp*) together constituting the *gynœcium* or *pistil*. Each carpel consists of an expanded, hollow, proximal

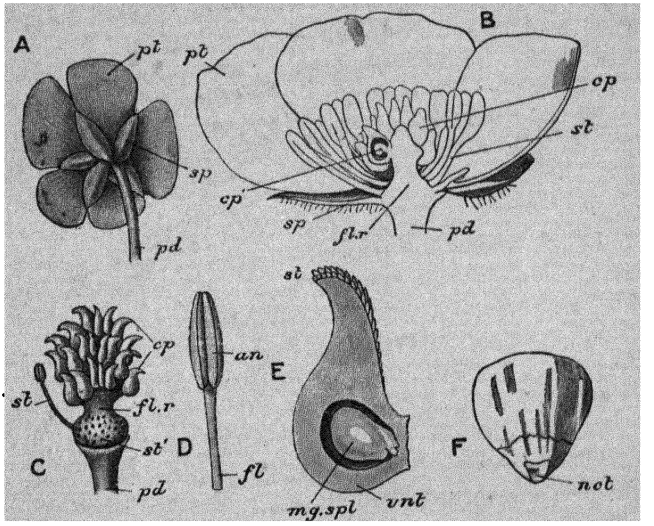

FIG. 124.—Structure of the flower of the Buttercup.

A, the entire flower from below, showing peduncle (*pd*), sepals (*sp*), and petals (*pt*).

B, vertical section of flower, showing peduncle (*pd*), floral receptacle (*fl. r*), sepals (*sp*), petals (*pt*), stamen (*st*), and carpels (*cp*).

The carpel *cp'* is cut vertically, and shows the megasporangium.

C, floral receptacle (*fl. r*), with carpels (*cp*), one stamen (*st*), and scars left by the removal of the remaining stamens.

D, stamen, showing filament (*fl*) and anther (*an*).

E, carpel in vertical section, showing venter (*vnt*) with contained megasporangium (*mg. spg*), and style (*st*).

F, petal, with nectary (*nct*).

(A and C, after Vines; B, D, and F, after Maout and Decaisne; E, after Oliver.)

portion or *venter*[1] (E, *vnt*), and of a short, hook-like distal extremity (*st*) covered with sticky hairs and called the *stigma*.

[1] Commonly called *ovary*.

The venter contains a single ovule or megasporangium (*mg. spg*), differing from that of the pine in being covered by a double instead of a single coat (Fig. 126, D, f^1, f^2), both perforated by a micropyle (*m. py*), which places the central mass of tissue or nucellus (*ncl*) in communication with the cavity of the venter (Fig. 126, A). The nucellus, like that of pines, contains a single embryo-sac or megaspore (*mg. sp*).

The fact that the megasporangia are contained in a cavity of the carpel, and so shut off from all direct communication with the exterior, forms a fundamental difference between the angiospermous or covered-seeded, and the gymnospermous or naked-seeded Phanerogams.

We saw that in Gymnosperms, as in the Vascular Cryptogams, the sporangia were borne on structures, the sporophylls, which were obviously modified leaves. In the buttercup the stamens and carpels have departed so widely from the leaf-type that their true nature becomes obvious only after comparison with other forms.

In the White Water-lily (*Nymphæa alba*) the very numerous petals are arranged, like the stamens, in a spiral, and the two sets of organs pass insensibly into one another. As we trace the petals (Fig. 125, A^1) upwards on the floral receptacle we find them become narrower in proportion to their breadth (A^2), and on the apex two little yellow lobes appear (*mi. spg*). Still passing up the spiral the lobes become more and more pronounced, and the petal narrower (A^3), until at last the lobes become aggregated into an undoubted anther (A^4, *an*), while the blade of the petal is narrowed to a filament, its distal end serving to unite the anther-lobes and constituting the *connective* (*cor*).

The same transition from petals to stamens is seen in many "double" flowers, such as the double apple, in which the number of petals becomes greatly increased by the

assumption of a petaloid form by the outer stamens, various intermediate stages being present from the typical stamen, through irregular leaves with anther-lobes at their distal ends, to the ordinary broad white petal.

We see, then, that a stamen is a leaf on the surface of which four microsporangia (B^1, *mi. spg*) are developed: the blade of the leaf is narrowed to form a mere stalk, while the

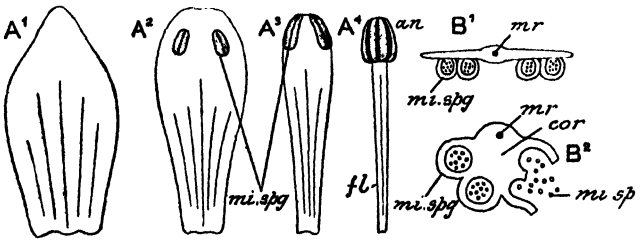

FIG. 125.— A^1–A^4, transition from petal to stamen: *mi. spg*, microsporangia; *fl*, filament; *an*, anther.

B^1, transverse section of male sporophyll in the stage A^2; *mr*, midrib of staminal leaf; *mi. spg*, microsporangia.

B^2, transverse section of typical anther, showing connective (*cor*) with vascular bundle or midrib (*mr*), on the left two microsporangia (*mi. spg*), and on the right the escape of the microspores (*mi. sp*) by dehiscence of the anther.

microsporangia have become so closely aggregated as to form a single four-lobed body, the anther (B^2).

Similarly the carpel can be shown to conform to the leaf-type. The flower of the cherry has a single flask-shaped carpel, consisting of a rounded venter, with an expanded stigma borne on the end of a stalk or *style*. But when the cherry flower becomes double, the normal carpel is replaced by a little green leaf, quite like a foliage-leaf, except that it is permanently folded upon the midrib so as to bring the two halves of its upper or dorsal surface almost into contact.

Imagine one or more of the marginal lobes of such a leaf to be replaced by megasporangia, as in Cycas (Fig. 122, E), and the edges of its proximal part to come together and unite (Fig. 126, B^1, B^2). The result will be the enclosure of the ovules in a capsule formed from the proximal part of the leaf, while its distal end forms the style and stigma.

The extreme differentiation of both male and female sporophylls is not the only important difference between the angiospermous and the gymnospermous flower. Almost equally characteristic, and equally striking as a sign of advance in organisation, is the fact that the sporophylls are surrounded by two sets—sometimes reduced to one—of floral organs, the sepals and petals, which together form the floral envelope or *perianth.* In most Gymnosperms the only indication of a perianth is in the form of inconspicuous barren scales, *i.e.*, scales not bearing sporangia, at the base of the cone (Fig. 119, A and B, *per*), while in Angiosperms the perianth has become differentiated into two well-marked and conspicuous sets of leaves.

The function of the sepals is usually to protect the other parts of the flower in the bud: they are generally of such a size as completely to close over the petals, stamens, and carpels until the flower opens, when they often either turn back or fall off. They are therefore to be looked upon as leaves which have been modified for protective purposes.

The petals serve an entirely different function. They are usually large and brightly coloured, forming the most conspicuous part of the flower: they are also commonly scented, and from them or some adjacent part nectar is secreted. This fluid forms the staple food of many insects, especially butterflies, moths, and bees, which, as soon as a flower is opened, may be seen to visit it and to insert head or proboscis in order to suck the sweet juice.

By the time this takes place the stamens have *dehisced*, *i.e.*, split down each side, so that the two pollen-sacs of each half-anther discharge their pollen by a common slit (Fig. 125, B²). The pollen is usually not dry like that of Gymnosperms but sticky, so that the grains are not readily blown away but tend to adhere to one another and to the ruptured anther. Thus, when the insect inserts its head into the flower a greater or less quantity of pollen is certain to stick to it, and to be carried off as the insect flies to another flower.

It will be remembered that the stigma is covered with sticky hairs, the consequence of which is that as the insect flies from flower to flower, the pollen it has collected from the stamens of one is transferred to the stigmas of another, and thus, in all the higher Angiosperms, pollination is effected by the agency of insects and not, as in Gymnosperms, by the chance action of the wind.

Thus the corolla serves an attractive purpose: by its colour and scent insects are informed of the store of nectar it contains, and in the search for that food they unconsciously benefit the plant by performing the work of pollination. In this way pollination is made more certain than when left to the wind, and the plant is saved the production of the immense quantity of pollen essential to a wind-fertilised plant, in which a very small fraction of the grains produced can possibly find their way to a female cone.

Still another striking feature of the angiospermous as compared with the gymnospermous flower is the shortening of its axis. A comparison of Fig. 126, A, with Fig. 119, A and C, shows that the floral receptacle (*fl. r*) of the Angiosperm is nothing but the axis of the gymnospermous cone shortened and broadened. The natural result is the suppression of the internodes and the consequent approximation

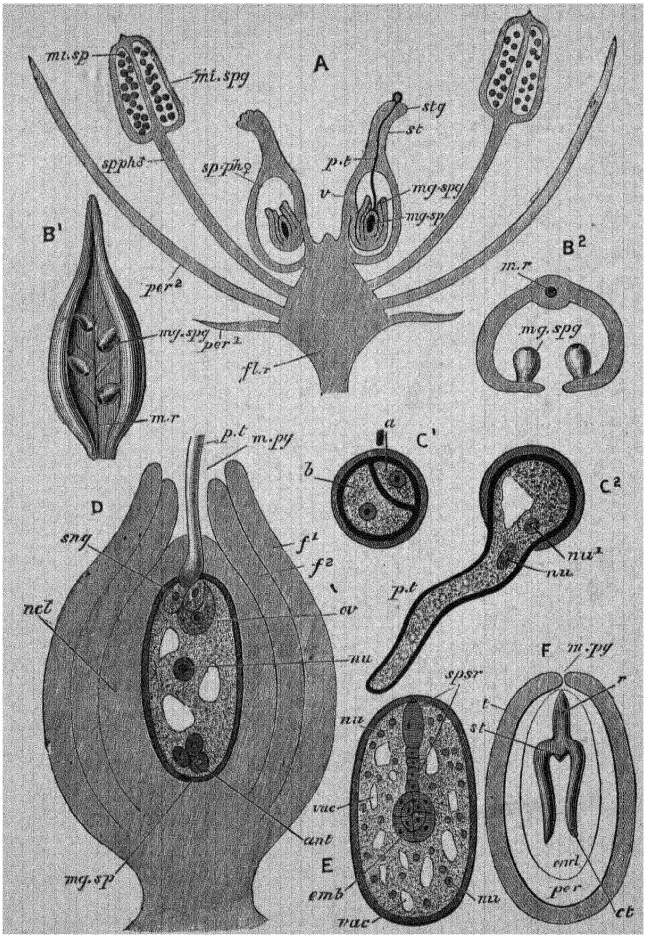

FIG. 129. —Reproduction and Development of Angiosperms.

A, diagrammatic vertical section of a flower consisting of an abbreviated axis or floral receptacle (*fl. r*) bearing a proximal (*per*[1]) and a distal (*per*[2]) whorl of perianth leaves (sepals and petals), a whorl of male sporophylls or stamens (*sp. ph.* ♂), and one of female sporophylls or carpels (*sp. ph.* ♀).

The male sporophyll bears microsporangia (*mi. spg*) containing microspores (*mi. sp*).

The female sporophyll consists of a solid style (*st*) terminated by a stigma (*stg*), and of a hollow venter (*v*) containing a megasporangium (*mg. spg*) in which is a single megaspore (*mg. sp*).

On the right side a microspore is shown on the stigma, and has sent off a pollen-tube (*p. t*) through the tissue of the style to the micropyle of the megasporangium.

B[1], diagram of a female sporophyll from the dorsal aspect, and B[2], the same in transverse section, showing the folding in of its edges to form the cavity or venter in which the megasporangia (*mg. spg*) are enclosed: *m. r*, the midrib.

C[1], a microspore, showing the two cells (*a* and *b*) into which its contents divide; the larger is the vegetative-cell.

C[2], the same, sending out a pollen-tube (*p. t*); *nu*, *nu*[1], the two nuclei: the generative nucleus has not yet divided.

D, diagrammatic vertical section of a megasporangium, showing the double integument (*f*[1], *f*[2]), nucellus (*ncl*), micropyle (*m. py*), and megaspore (*mg. sp*): the latter contains the secondary nucleus (*nu*) in the centre, three antipodal cells (*ant*) at the proximal end, and two synergidæ (*sng*) and an ovum (*ov*) at the distal end.

A pollen-tube (*p. t*) is shown with its end in contact with the synergidæ.

E, semi-diagrammatic section of the megaspore of a young seed, showing an embryo (*emb*) in the polyplast stage with its suspensor (*spsr*); also numerous vacuoles (*vac*) and nuclei (*nu*).

F, diagrammatic vertical section of a ripe seed, showing the seed-coat (*t*), micropyle (*m. py*), perisperm (*per*) derived from the tissue of the nucellus, and endosperm (*end*) formed in the megaspore and containing an embryo in the phyllula stage with stem-rudiment (*st*), cotyledons (*ct*), and root (*r*).

(B[1], after Behrens; C[1], C[2], and E, altered from Howes.)

of the nodes, so that all the leaves—sepals, petals, stamens, and carpels—arise close together from a small area. Thus, the angiospermous flower, like the gymnospermous cone, is a modified shoot of limited growth, having its axis shortened to a floral receptacle and its leaves modified to form the various floral organs. The composition of the flower may therefore be expressed in a diagrammatic form as follows:—

Floral Receptacle = Axis of Shoot } – Leaves { Perianth { Protective—Sepals (Calyx). / Attractive—Petals (Corolla). } Sporophylls { Male—Stamens (Androecium). / Female—Carpels (Gynœcium). }

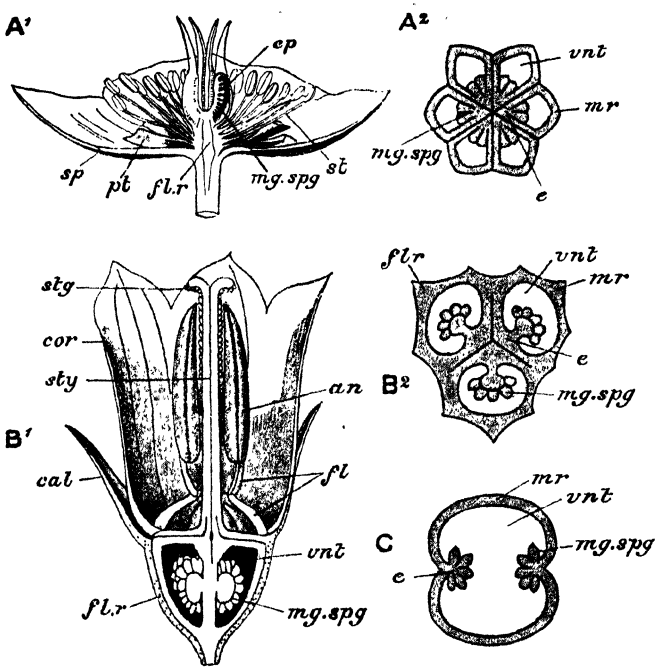

FIG. 127.—A¹, Vertical section of flower of *Helleborus*, showing *fl. r*, floral receptacle ; *sp*, sepals ; *pt*, petals ; *st*, stamens ; and *cp*, carpels, that to the right cut longitudinally to show the megasporangia (*mg. spg*).

A², transverse section of gynœcium of Helleborus passing through the venter (*vnt*) of the six carpels, each of which has a midrib (*mr*) and united edges (*e*) to which the megasporangia are attached.

B¹, vertical section of flower of *Campanula*, showing floral receptacle (*fl. r*) enclosing venter of gynœcium (*vnt*), with megasporangia (*mg. spg*) ; calyx (*cal*) ; corolla (*cor*) ; anthers (*an*) and filaments (*fl*) of stamens ; and style (*sty*) and stigma (*stg*).

B², transverse section of gynœcium of *Campanula* enclosed in floral receptable (*fl. r*). Letters as in A².

C, transverse section of gynœcium of *Ribes*. Letters as in A².

(A¹ and B¹, after Le Maout and Decaisne.)

There are one or two important modifications of the flower which must be briefly referred to.

In the Christmas-rose (*Helleborus*) the general structure of the flower resembles that of the buttercup except that the petals (Fig. 127, A[1], *pt*) are small and tubular, and the sepals (*sp*) so large as to form the obvious and attractive part of the flower. But the large carpels (*cp*) are few—three to six—in number, arranged in a single whorl, and closely applied to one another by their lateral faces (A[2]). The peripheral or outwardly-facing border of each represents the midrib (*mr*) of the carpellary leaf, the central border—that facing the axis of the flower—its united edges (*e*). To the latter are attached several megasporangia arranged in a longitudinal row.

In the Canterbury-bell (*Campanula*) there appears at first sight to be a single carpel (B[1] *vnt*) with three stigmas (*stg*). But a transverse section of the venter (B[2]) shows it to contain three cavities arranged round a longitudinal axis to which are attached three rows of ovules (*mg. spg*), one to each chamber. Obviously such a pistil is produced by the three carpels of which it is composed being not simply applied to one another as in the Christmas-rose, but actually fused. In the currant (*Ribes*) the pistil shows in transverse section a single cavity only (C), but with two rows of ovules (*mg. spg*): here the carpellary leaves have united with one another simply by their edges.

Campanula illustrates concrescence not of the carpels only but of all the other floral whorls. The sepals have united to form a cup-like calyx (Fig. 127, B[1], *cal*), the petals are joined into a vase-like corolla (*cor*), and the filaments of the stamens (*fl*) are united below. Moreover, the floral receptacle (*fl. r*) instead of being conical, as in the buttercup, is hollowed into a cup which encloses and is fused with

the venter of the pistil (*vnt*): it thus loses all appearance of being a stem-structure and becomes a mere capsule for the gynœcium, giving attachment at its edges to the other floral organs.

An extended study of flowers will show how all the main modifications are brought about by the varying form of the floral receptacle, by the concrescence of one part with another, by the enlargement of certain parts, and by the diminution or complete suppression of others.

The microspores are at first simple cells, each with a double cell-wall and a nucleus. The nucleus divides into two (Fig. 126, c^1), a larger vegetative nucleus, and a smaller which divides again forming two generative nuclei, each surrounded by its layer of protoplasm.

No prothallus is formed in the megaspore, but its nucleus divides, the products of division pass to opposite ends of the spore, and each divides again and then again, so that four nuclei are produced at each extremity. Three of the nuclei at the proximal end—that furthest from the micropyle —become surrounded by protoplasm and take on the character of cells (D, *ant*) all devoid of cell-wall and called *antipodal cells*; the fourth remains unchanged. Similarly, of the four nuclei at the distal or micropylar end, one remains unchanged and three assume the form of cells by becoming invested with protoplasm. Of these three, two lie near the wall of the megaspore and are called *synergidæ* (*sng*): the third, more deeply placed, is the ovum (*ov*). The two unaltered nuclei now travel to the centre of the megaspore and unite with one another, forming the *secondary nucleus* (*nu*) of the spore.

There is thus a single ovum produced in each megaspore, but no ovary and no prothallus: the female portion of the gamobium is reduced to its simplest expression.

Pollination may take place, as we have seen, by the agency either of the wind or of insects. The microspores are deposited on the stigma (A), where they germinate, each sending off a pollen-tube (A and c^2, *p. t*), which grows downwards through the tissue of the stigma and style to the cavity of the venter, where it reaches a megasporangium, and entering at the micropyle (D, *p. t*), continues its course through the nucellus, finally applying itself to the distal end of the megaspore in the immediate neighbourhood of the synergidæ.

In the meantime the nuclei of the microspore (c^2, *nu*, nu^1) have passed into the end of the pollen-tube. The vegetative nucleus undergoes degeneration, becoming shrivelled and unaffected by dyes. The generative nuclei wander to the apex of the pollen-tube and ultimately pass through the softened cell-wall of its swollen end, one of them entering the ovum and uniting with its nucleus in the usual way, while the other fuses with the secondary nucleus of the megaspores.

The ovum is thus converted into an oosperm or unicellular embryo: it acquires a cell-wall and almost immediately divides into two cells, of which that nearest the micropyle becomes the suspensor (E, *spsr*), the other, or embryo proper (*emb*), forming a solid aggregate of cells, the polyplast. By further differentiation rudiments of a stem (F, *st*), a root (*r*) and either one or two cotyledons (*ct*) are formed, and the embryo passes into the phyllula stage.

While the early development of the embryo is going on, the secondary nucleus of the megaspore divides repeatedly, and the products of division (E, *nu*) becoming surrounded by protoplasm, a number of cells are produced, which, by further multiplication, fill up all that part of the megaspore which is not occupied by the embryo. The tissue thus

formed is called the endosperm (F, *end*), and occupies precisely the position of the vestigial prothallus of Gymnosperms (Fig. 119, p. 453, D, *prth*, and E, *end*: and p. 458), differing from it in the fact that it is formed only after fertilisation. We have here a case of retarded development: the degeneration of the prothallus has gone so far that it arises long after the formation of the ovum which, in both Gymnosperms and Vascular Cryptogams, is a specially modified prothallial cell. As a rule the tissue of the nucellus disappears as the embryo grows, but in some cases, *e.g.*, the water-lily, it is retained, forming an additional store of nutrient material and called the *perisperm* (Fig. 126, F, *per*).

The phyllula continues to grow and remains inclosed in the megasporangium, which undergoes a corresponding increase in size and becomes the seed. One or more seeds also remain inclosed in the venter of the pistil, which grows considerably and constitutes the *fruit*. Finally the seeds are liberated, the phyllula protrudes first its root, and then its stem and cotyledons, through the ruptured seed-coat, and becomes the seedling plant.

We learn from this and the two preceding lessons that there is a far greater uniformity of organisation among the higher plants than among the higher animals, not only in anatomical and histological structure, but also in the fact that alternation of generations is universal from mosses up to the highest flowering plants. But as we ascend the series, the gamobium sinks from the position of a conspicuous leafy plant to that of a small and insignificant prothallus, becoming finally so reduced as to be recognisable as such only by comparison with the lower forms.

SYNOPSIS

A.—AN ACCOUNT OF THE STRUCTURE, PHYSIOLOGY, AND LIFE-HISTORY OF A SERIES OF TYPICAL ORGANISMS IN THE ORDER OF INCREASING COMPLEXITY.

I.—The Simpler Unicellular Organisms.

1 *Amœba.*

PAGE

Cell-body amœboid or encysted: cell-wall nitrogenous (?): nutrition holozoic: reproduction by simple or binary fission 1

2. *Hæmatococcus.*

Cell-body ciliated or encysted: cell-wall of cellulose: nutrition holophytic: reproduction by binary fission . . 23

3. *Heteromita.*

Cell-body ciliated: nutrition saprophytic: asexual reproduction by binary fission: sexual reproduction by conjugation of equal and similar gametes followed by multiple fission of the protoplasm of the zygote, forming spores . 36

4. *Euglena.*

Cell-body ciliated or encysted: cell-wall of cellulose: mouth and gullet present: nutrition holophytic and holozoic: reproduction by binary and multiple fission. . 44

5. *Protomyxa.*

Cell-body amœboid, ciliated, or encysted: plasmodia formed by concrescence of amœbulæ: cell-wall nitrogenous (?): nutrition holozoic: reproduction by multiple fission of encysted plasmodium 49

PAGE

6. *Mycetozoa.*
Like Protomyxa, but owing to the presence of nuclei the relation of the individual cell-bodies to the plasmodium is more clearly seen: cell-wall of cellulose 52

7. *Saccharomyces.*
Cell-body encysted: cell-wall of cellulose: nutrition saprophytic; reproduction by gemmation or by internal fission: acts as an organised ferment 71

8. *Bacteria.*
Cell-body ciliated or encysted: cell-wall of cellulose: nutrition saprophytic: reproduction by binary fission or by spore-formation: act as organised ferments: the simplest and most abundant of organisms 82

II.—UNICELLULAR OR NON-CELLULAR ORGANISMS IN WHICH THERE IS CONSIDERABLE COMPLEXITY OF STRUCTURE ACCOMPANIED BY PHYSIOLOGICAL DIFFERENTIATION.

a. Complexity attained by differentiation of cell-body.

9. *Paramæcium.*
Medulla, cortex, and cuticle: trichocysts: complex contractile vacuoles: mega- and micro-nucleus: mouth, gullet, and anal spot: conjugation temporary, no zygote being formed, but interchange of nuclear material during temporary union 106

10. *Stylonychia.*
Extreme differentiation or heteromorphism of cilia . . . 116

11. *Oxytricha.*
Fragmentation of nucleus 120

12. *Opalina.*
Multinucleate but non-cellular: parasitism and its results: necessity for special means of dispersal of an internal parasite 121

13. *Vorticella.*
A stationary organism: limitation of cilia to defined regions: muscle-fibre in stalk: necessity for means of dispersal in a fixed organism: conjugation between free-swimming micro- and fixed mega-gamete: zygote indistinguishable from a zooid of the ordinary kind 126

PAGE

14. *Zoothamnium.*
A compound organism or colony with dimorphic (nutritive and reproductive) zooids: begins life as a single zooid 134

b. Complexity attained by differentiation of cell-wall or by formation of skeletal structures in the protoplasm.

15. *Foraminifera.*
Calcareous shells (cell-walls) of various and complicated form 148

16. *Radiolaria.*
Membranous perforated shell (cell-wall) and external silicious skeleton often of great complexity: symbiotic relations with Zooxanthella 152

17. *Diatoms.*
Silicious, two-valved, highly-ornamented shells 155

Complexity attained by simple elongation and branching of the cell.

18. *Mucor.*
A branching filamentous non-cellular fungus: necessity for special reproductive organs in such an organism: they may be sporangia producing asexual spores, or equal and similar gametes producing a resting zygote 158

19. *Vaucheria.*
A branched filamentous non-cellular alga: clear distinction between the gametes or conjugating bodies and the sexual reproductive organs or gonads in which they are produced: gonads differentiated into male (spermary) and female (ovary): gametes differentiated into male (sperm) and female (ovum): zygote an oosperm 169

20. *Caulerpa.*
Illustrates maximum differentiation of a non-cellular plant: stem-like, leaf-like, and root-like parts 174

III.—ORGANISMS IN WHICH COMPLEXITY IS ATTAINED BY CELL-MULTIPLICATION, ACCOMPANIED BY NO OR BUT LITTLE CELL-DIFFERENTIATION.

a. Linear aggregates.

21. *Penicillium.*
A multicellular, filamentous, branched fungus: mycelial, submerged, and aërial hyphæ: apical growth: abundant production of spores by constriction of aërial hyphæ . . 184

PAGE

22. *Agaricus.*
Complexity attained by interweaving of hyphæ in a definite form: illustrates maximum complexity of a linear aggregate 191

23. *Spirogyra.*
A multicellular filamentous unbranched alga: interstitial growth: gonads equal and similar, but gametes show first indications of sexual differentiation. 194

b. Superficial aggregate.

24. *Monostroma.*
Cell-division takes place in two dimensions 201

c. Solid aggregate.

25. *Ulva.*
Like Monostroma, but cell-division takes place in three dimensions 203

IV.—SOLID AGGREGATES IN WHICH COMPLEXITY IS INCREASED BY A LIMITED AMOUNT OF CELL-DIFFERENTIATION.

26. *Nitella.*
Segmented axis: nodes and internodes: appendages—leaves and rhizoids: apical growth by binary fission of apical cell accompanied by immediate division and differentiation of newly-formed segmental cells: complex gonads (ovaries and spermaries) 203

27. *Hydra.*
Example of a simple diploblastic animal: cells arranged in two layers (ecto- and endoderm) enclosing an enteron which opens externally by the mouth: combination of intra-cellular with extra-cellular or enteric digestion . . 218

28. *Bougainvillea.*
Example of a colony with diploblastic zooids which are nutritive (hydranths) and reproductive (medusæ): differentiation of a rudimentary mesoderm producing imperfect tripoblastic condition: central and peripheral nervous system: alternation of generations, a gamobium (the medusa) alternating with an agamobium (the hydroid colony); significance of developmental stages—oosperm (unicellular), polyplast (multicellular but undifferentiated), and planula (diploblastic) 234

PAGE

29. *Diphyes.*
A free-swimming colony with polymorphic (nutritive, reproductive, protective, and natatory) zooids 248

30. *Porpita.*
Extreme polymorphism of zooids giving the colony the character of a single physiological individual 249

V.—SOLID AGGREGATES IN WHICH CELL-DIFFERENTIATION, ACCOMPANIED BY CELL-FUSION, TAKES AN IMPORTANT PART IN PRODUCING GREAT COMPLEXITY IN THE ADULT ORGANISM.

31. *Polygordius.*
A triploblastic, cœlomate animal with metameric segmentation: prostomium, peristomium, metameres, and anal segment: besides ecto- and endoderm there is a well developed mesoderm divided into somatic and splanchnic layers separated by the cœlome: differentiation of cells into fibres, &c.: muscle-plates formed as cell-fusions: necessity for distributing system for supply of food to parts of the body other than the enteric canal, and for the removal of waste matters:—circulatory, respiratory, and excretory systems: high development of nervous system—brain and ventral cord, afferent and efferent nerves: characteristic developmental stages—oosperm, polyplast, gastrula (diploblastic), trochosphere (diploblastic with stomodæum and protodæum), late trochosphere (triploblastic but acœlomate) 268

32. *Mosses.*
Cell-differentiation very slight, but the type necessary to lead up to ferns: sclerenchyma and axial bundle: distributing system rendered necessary by carbon dioxide being taken in by the leaves, water and mineral salts by the rhizoids: alternation of generations—the leafy plant is the gamobium, the agamobium being represented by the spore-producing sporogonium: developmental stages—oosperm and polyplast, the latter becoming highly differentiated to form the sporogonium 400

33. *Ferns.*
Extensive cell-differentiation: formation of fibres (elongated cells) and vessels (cell-fusions); general differentiation of tissues into epidermis, ground-parenchyma, and vascular bundles: presence of true roots: the leafy plant is the agamobium and produces spores from which the gamobium, in the form of a small prothallus, arises: developmental stages—oosperm, polyplast, and phyllula (leaf- and root-bearing stage) 412

PAGE

VI.—Brief Descriptions of Examples of the Higher Groups of Animals and Plants.

a. ANIMALS.

All are triploblastic and cœlomate.

34. *Starfish.*

Radially symmetrical: discontinuous dermal exoskeleton: characteristic organs of locomotion (tube feet) in connection with ambulacral system of vessels 306

35. *Crayfish.*

Metamerically segmented: segmented lateral appendages: differentiation of metameres and appendages: continuous cuticular exoskeleton discontinuously calcified: gills as paired lateral offshoots of the body-wall: heart as muscular dilation of dorsal vessel: cœlome greatly reduced and its place taken by an extensive series of blood-spaces: nervous system sunk in the mesoderm and consisting of brain and ventral nerve-cord 318

36. *Mussel.*

Non-segmented: mantle formed as paired lateral outgrowths of dorsal region: foot as unpaired median outgrowth of ventral region: cuticular exoskeleton in the form of a calcified bivalved shell: gills as paired lateral outgrowths of body-wall: heart as muscular dilatation of dorsal vessel: cœlome reduced to pericardium: nervous system consists of three pairs of ganglia sunk in the mesoderm 348

37. *Dogfish.*

Metamerically segmented: differentiated into head, trunk, and tail: trunk alone cœlomate in adult: appendages as median (dorsal, ventral, and caudal) and paired (pectoral and pelvic) fins: discontinuous dermal exoskeleton and extensive endoskeleton of partially calcified cartilage, including a chain of vertebral centra below the nervous system replacing an embryonic notochord: gills as pouches of pharynx opening on exterior: heart as muscular dilatation of ventral vessel: hollow dorsal nervous system not perforated by enteric canal. 366

b. PLANTS.

All exhibit alternation of generations and the series shows the gradual subordination of the gamobium to the agamobium.

PAGE

38. *Equisetum.*
Sporangia borne on sporophylls arranged in cones: spores homomorphic: prothalli dimorphic (male and female) 434

39. *Salvinia.*
Spores dimorphic: microspore produces vestigial male prothallus: megaspore produces greatly reduced female prothallus 438

40. *Selaginella.*
Microspore produces unicellular prothallus and multicellular spermary, both endogenously: female prothallus formed in megaspore and is almost endogenous: embryo provided with suspensor 442

41. *Gymnosperms.*
Cones dimorphic (male and female), with rudimentary perianth: no sperms formed but microspore gives rise to pollen tube, nuclei in which are the active agents in fertilisation: single megaspore permanently enclosed in each megasporangium: female prothallus purely endogenous: embryo (phyllula) remains enclosed in megasporangium which becomes a seed 447

42. *Angiosperms.*
Cone modified into flower by differentiation of sporophylls and perianth: female sporophyll forms closed cavity in which megasporangia are contained: megaspore produces a single ovary represented simply by an ovum and two synergidæ: formation of prothallus retarded until after fertilisation 461

B.—SUBJECTS OF GENERAL IMPORTANCE DISCUSSED IN SPECIAL LESSONS.

I.—Cells and Nuclei.

a. The higher plants and animals contain cells similar in structure to entire unicellular organisms, and like them existing in either the amœboid, ciliated, encysted, or plasmodial condition 56

b. Minute structure of cells:—cell-protoplasm, cell-membrane, nuclear membrane, nuclear sap, chromatin 62

c. Direct and indirect nuclear division 65

PAGE

d. The higher plants and animals begin life as a single cell, the ovum 68

II.—Biogenesis.

a. Definition of biogenesis and abiogenesis: brief history of the controversy 95

b. Crucial experiment with putrescible infusions: sterilisation: germ-filters: occurrence of abiogenesis disproved under known existing conditions 98

III.—Homogenesis.

Definition of homogenesis and heterogenesis; truth of the former firmly established 102

IV.—Origin of Species.

a. Meaning of the term Species: the question illustrated by a consideration of certain species of Zoothamnium 137

b. Definition of Creation and Evolution: hypothetical histories of Zoothamnium in accordance with the two theories . . 141

c. The principles of Classification: natural and artificial classifications 141

d. The connection between ontogeny and phylogeny 146

V.—Plants and Animals.

a. Attempt to define the words plant and animal, and to place the previously considered types in one or other kingdom 176

b. Significance of "third kingdom," Protista 182

VI.—Spermatogenesis and Oogenesis.

Origin of sperms and ova from primitive sex-cells: differences in structure and development of the sexual elements . . 253

VII.—Maturition and Impregnation.

a. Formation of first and second polar cells and of female pronucleus 257

b Entrance of sperm and formation of male pronucleus . . . 260

c. Conjugation of pronuclei 260

PAGE

VIII.—UNICELLULAR AND DIPLOBLASTIC ANIMALS.

In plants there is a clear transition from unicellular forms to solid aggregates, but in animals the connection of the gastrula with unicellular forms is uncertain 261

C.—Other matters of general importance, such as the composition and properties of protoplasm, cellulose, chlorophyll, starch, &c.: metabolism: holozoic, holophytic, and saprophytic nutrition: intra- and extra-cellular digestion: amœboid, ciliary, and muscular movements: the elementary physiology of muscle and nerve: parasitism and symbiosis: asexual and sexual generation: and the elements of embryology —are discussed under the various types, and will be most conveniently referred to by consulting the Index.

INDEX AND GLOSSARY

INDEX AND GLOSSARY

A

Abdomen, Crayfish, 318

Abiogen'esis (*a*, not: *βίος*, life: *γένεσις*, origin), the origin of organisms from not-living matter: former belief in, 96

Absorption by root-hairs, 409, 422

Accre'tion (*ad*, to: *cresco*, to grow), increase by addition of successive layers, 14

Achrom'atin (*a*, not: *χρῶμα*, colour), the constituent of the nucleus which is unaffected or but slightly affected by dyes. See nuclear sap

Acœlom'ate (*a*, not: *κοίλωμα*, a hollow), having no cœlome (*q.v.*): 299

Adduct'or muscles, Mussel, 354

Aerob'ic (*ἀήρ*, air: *βίος*, life), applied to those microbes to which free oxygen is unnecessary, 93

Agamob'ium (*a*, not: *γάμος*, marriage: *βίος*, life), the asexual generation in organisms exhibiting alternation of generations (*q.v.*)

AGAR'ICUS (mushroom):—Figure, 192: general characters, 191: microscopic structure, 193: spore-formation, 193

Algæ (*alga*, sea-weed), 169, 432

Alternation of Generations, meaning of the phrase explained under Bougainvillea, 248: Moss, 408: Fern, 429: Equisetum, 438: Salvinia, 442: Selaginella, 446: Gymnosperms, 460: Angiosperms, 476

Ambula'cral (*ambulacrum*, a walking place) groove, 307: ossicles, 308: **system**, starfish, 309—313

AMŒB'A (*ἀμοιβός*, changing):—Figure, 2: occurrence and general characters, 1: movements, 4, 9: species of, 8: resting condition, 10: nutrition, 11: growth, 13: respiration, 17: metabolism, 17: reproduction, 19: immortality, 20: conjugation, 20: death, 20, 21: conditions of life, 21: animal or plant? 180

Amœb'oid movements, 4

Amœb'ula (diminutive of Amœba), the amœboid germ of one of the lower organisms, 51, 54

Anab'olism (*ἀναβολή*, that which is thrown up). See Metabolism, constructive.

Anaerob'ic (*a*, not: *ἀήρ*, air: *βίος*, life), applied to those microbes to which free oxygen is unnecessary, 93

An'al (*ἄνυς*, the vent) **segment**, Polygordius, 270

An'al spot, Paramœcium, 113

An'astates (*ἀνάστατος*, from *ἀναστῆναι*, to rise up) See Mesostates, anabolic.

Anatomy (*ἀνατέμνω*, to cut up), the study of the structure of organisms as made out by dissection, 289

Andrœ'cium (*ἀνήρ*, a male: *οἶκος*, a dwelling), the collective name for the male sporophylls in the flower of Angiosperms, 464, 471

AN'GIOSPERMS (*ἀγγεῖον*, a vessel: *σπέρμα*, seed):—Figures, 462, 465, 467, 470, 472: general characters, 461: structure of flower, 463: reduction of gamobium, 474: pollination and fertilization, 469, 475: formation of fruit and seed, and development of the leafy plant, 476

Animal, definition of, 179

Animals, classification of, 320

Animals and Plants, comparison of type forms, 176: discussion of doubtful forms, 180

Animals, Protists, and Plants, boundaries between artificial, 182

Annual Rings, 450

Anodonta (*a* not: *ὀδους*, a tooth). See Mussel

Antenna (*antenna*, a sail-yard), 325

Antennary Gland. See Kidney

Antennule (dim. of antenna), 325

Anther, 454, 464, 466

Antherid'ium. See Spermary.

Antherozo'id. See Sperm.
Antip'odal cells, 474
An'us (*anus*, the vent), the posterior aperture of the enteric canal, 270
Ap'ical cell:—Penicillium, 190: Nitella, 208: Moss, 403: stem of Fern 418: root of Fern, 421: prothallus of Fern, 425
Ap'ical cone, Fern, 418
A'pical growth, 190, 419
A'pical mer'istem, a mass of meristem (*q.v.*) at the apex of a stem or root, 418, 421
Appen'dages, lateral:—crayfish, 321: dogfish, 369
Archegon'ium (*ἀρχή*, beginning: *γόνος*, production), the name usually given to the ovary of the higher plants
Aristotle, abiogenesis taught by, 96
Arteries, Crayfish, 337: Dogfish, 384
Arthrobranchia (*ἄρθρον*, a joint: *βράγχια*, gills), 337
Anthropoda, the, 306
Artificial reproduction of Hydra, 231
Asexual generation. See Agamobium.
Asexual reproduction. See Fission, Budding, Spore.
Asparagin, 410
Assimila'tion (*assimilo*, to make like), the conversion of food materials into living protoplasm, 13
Ast'acus. See Crayfish.
Asterias. See Starfish.
Astrosphere, 65
Atrophy (*a*, without: *τροφή*, nourishment), a wasting away, 118
Auditory organ, Crayfish, 342: Mussel, 363: Dogfish, 395
Aur'icle. See Heart.
Autom'atism (*αὐτόματος*, acting of one's own will), 10, 244
Axial Bundle, Moss, 403
Axial fibre, Vorticella, 129
Axil (*axilla*, the arm-pit), 206
Axis, primary and secondary, 206

B

BACIL'LUS (*bacillum*, a little staff), 85 Figure, 87
BACTER'IA (*βακτήριον*, a little staff) or **MICROBES** (*μικρός*, small: *βίος*, life):—occurrence, 82: structure of chief genera, 84: reproduction, 87: nutrition, 89: ferment-action, 91; parasitism, 92: conditions of life, 92: presence in atmosphere, 102: animals or plants? 182
BACTERIUM termo (Figures) 83, 84
Baer, von, Law of Development, 43
Barnacle-geese, supposed heterogenetic production of, 103
Bark. See Cortex.
Bast. See Phloëm.
Binom'inal nomenclature, 8, 139
Biogen'esis (*βίος*, life: *γένεσις*, origin), the origin of organisms from pre-existing organisms, 96: former belief in, 96: early experiments on, 97: crucial experiment on, 98
Biol'ogy (*βίος*, life: *λόγος*, discussion), the science which treats of living things
Bipinnaria, larva of Starfish, 317
Blast'ocœle (*βλαστός*, a bud: *κοῖλον*, a hollow), the larval body-cavity, 295
Blood, Polygordius, 280: Crayfish, 341: Mussel, 362: Dogfish, 390
Blood-corpuscles: colourless, see Leucocytes: red, 56, 390: Figures, 57
Blood-vessels, Polygordius, 282: development of, 302: Starfish, 314: Crayfish, 337: Mussel, 360: Dogfish, 384
Body-cavity. See Blastocœle and Cœlome.
Body-segments. See Metameres.
BOUGAINVILLEA (after L. A. de Bougainville, the French navigator:—Figure, 233. occurrence and general characters, 234: microscopic structure, 236: structure of medusa, 239: structure and functions of nervous system, 242: organs of sight, 244: reproduction and development, 245: alteration of generations, 248
Bract (*bractea*, a thin plate), 249
Brain:—Polygordius, 283: trochosphere, 296: Crayfish, 341: Dogfish, 391
Branch, Nitella, 206
Branch'ia (*βράγχια*, gill). See Gill.
Branch'ial apertures, Dogfish, 368, 381, 383
Browne, Sir Thomas, on abiogenetic origin of mice, 96
Buc'cal (*bucca*, the cheek) **groove**, Paramœcium, 109
Bud, budding, Saccharomyces, 73: comparison of with fission, 73: Hydra, 233
Bundle-sheath. See Endodermis.
Buttercup, flower, 464 (Figure)

C

Calyp'tra (*καλύπτρα*, a veil), 407
Cal'yx (*κάλυξ*, the cup of a flower), the outer or proximal whorl of the perianth in the flower of Angiosperms, 464, 471, 473
Cambium, 450
Canals, radial and circular, medusa, 239
Canal-cells of ovary, 405, 426
Cap-cells of roots, 422
Carapace, Crayfish, 318
Carbon dioxide, decomposition of by chlorophyll bodies, 29
Cardiac division. See Stomach.
Car'pel (*καρπός*, fruit), a female sporophyll, 455, 456, 464, 467
Cartilage, 372
CAULER'PA (*καυλός*, a stem: *ἕρπω*, to creep), 175 (Figure)
Cell (*cella*, a closet or hut, from the first

conception of a cell having been derived from the walled plant-cell, :—meaning of term, 61 : minute structure of (Figure), 62 : varieties of (Figure), 57
Cell-aggregate, meaning of term, 188.
Cell-colony :—temporary, Saccharomyces, 73 : permanent, Zoothamnium, 135
Cell-division, 65 (Figure)
Cell-fusion 302, 419
Cell-layer, 222, 273
Cell-membrane or **wall**, 10, 27, 63
Cell-multiplication and **differentiation**, 215 : Polygordius, 302 : Fern, 419
Cell-plate, 67
Cell-protoplasm, 62
Cell'ulose, composition and properties of, 28
Central capsule, Radiolaria, 152
Central particle or **Centrosome** (*κέντρον*, centre : *σῶμα*, the body), 65, 261 (Figure)
Ceph'alothor'ax (*κεφαλή*, head : *θώραξ*, breast-plate), Crayfish, 318
Cerebral ganglion. See Brain.
Cerebro-pleural ganglion, Mussel, 362
Cheliped (*χηλή*, claws : *πούς*, foot), 323
Chlor'ophyll (*χλωρός*, green : *φύλλον*, a leaf), the green colouring matter of plants, properties of, 26, 31 : occurrence in Bacteria, 87 : in Hydra, 228
Chrom'atin (*χρῶμα*, a colour), the constituent of the nucleus which is deeply stained by dyes, 7, 63 : male and female in nucleus of oosperm, 261
Chrom'atophore (*χρῶμα*, colour : *φέρω* to bear), a mass of proteid material impregnated with chlorophyll or some other colouring matter, 26, 46, 197, 207, 228
Chromosome (*χρῶμα*, colour : *σῶμα* body), 65, 66, 261
Cil'ium (*cilium*, an eye-lash), defined, 25*note* : comparison of with pseudopod, 34, 52 : absence of cilia in Arthropoda, 327
Cil'iary movement, 25 : a form of contractility, 33
Cil'iate Infusor'ia, 107
Circulatory organs, Polygordius, 282 : Crayfish, 337 : Mussel, 360 : Dogfish, 384
Classification, natural and artificial, 141 : natural, a genealogical tree, 145
Cnid'oblast (*κνίδη*, a nettle : *βλαστός*, a bud), the cell in which a nematocyst (*q.v.*) is developed, 227
Cnid'ocil (*κνίδη* and *cilium*), the "trigger-hair" of a cnidoblast, 227
Cœlenterata, the, 305
Cœlome (*κοίλωμα*, a hollow), the body-cavity :—Polygordius, 270 : Starfish, 306 : Crayfish, 335, 343 : Mussel, 355 : Dogfish, 372 : development of, Polygordius, 299
Cœlom'ate, provided with a cœlome, 273
Cœlomic epithelium. See Epithelium.
Cœlomic fluid, Polygordius, 278
Col'loids (*κόλλα*, glue : *εἶδος*, form), properties of, 6
Colony, Colonial organism, meaning of term, 135, 234 : formation of temporary colonies, Hydra, 231
Columel'la (a little column), 162
Com'missure (*commissūra*, a band), 279
Compound organism. See Colony.
Concres'cence (*cum*, together : *cresco*, to grow), the union of parts during growth
Cone, an axis bearing sporophylls :—Equisetum, 436 : Selaginella, 444 : Gymnosperms, 452
Conjuga'tion (*conjugātio*, a coupling), the union of two cells, in sexual reproduction :—Amœba, 20 : Heteromita, 41 : Paramœcium, 114 : Vorticella, 132 : Mucor, 165 : Spirogyra, 198 : of ovum and sperm, 260 : monœcious and dicœcious, 199 : comparison with plasmodium-formation, 54
Connective, œsophageal, 283, 341
Connective tissue, 329, 369
Contractile vac'uole (*vacŭus*, empty) :—Amœba, 8, 16 : Euglena, 47 : Paramœcium, 111
Contractil'ity (*contractio*, a drawing together), nature of, 10, 34 : muscular, 130
Contraction, physical and biological, 10
Conus arteriosus, 384
Cork, 449
Cork-cambium, 451
Coroll'a (*cŏrolla*, a little wreath), the inner or distal whorl of the perianth in the flower of Angiosperms, 464, 468, 471, 473
Corpuscles. See Blood-corpuscles, and Leucocytes.
Cortex, cor'tical layer (*cortex*, bark), Flowering plants, 59, 448 : Infusoria, 110, 126
Cotton-wool as a germ-filter, 99
Cotyle'don (*κοτύλη-δών*, a cup or socket), the first leaf or leaves of the phyllula (*q.v.*) in vascular plants, 427
Cran'ium (*κρᾶνίον*, the skull), 374
CRAYFISH :—Figure, 319 : general characters, 314, 315 : limited number and concrescence of metameres (Figure), 320 : appendages (Figure), 322 : exoskeleton, 319 : enteric canal (Figures), 322 : gills (Figure), 318 : blood-system (Figure), 335, 337 : kidney, 337 : nervous system, 319 : Muscles (Figures), 327 : reproductive organs, 343 : development, 343
Creation (*creo*, to produce), definition of, 141 : illustrated in connecton with species of Zoothamnium (Diagram), 142
Cross-fertilization : applied to the sexual process when the gametes spring from different individuals, 199

Cryst'alloids (*κρύσταλλος*, crystal : *εἶδος* form), properties of, 6
Cut'icle (*cuticula*, the outer skin), nature of in unicellular animals, 45, 109 : in multicellular animals, 238
Cyst (*κύστις*, a bag), used for cell-wall in many cases, 10, 51

D

Dallinger, Dr. W. H , observations on an apparent case of heterogenesis, 103
Daughter-cells, cells formed by the fission or gemmation of a mother-cell, 35, 67
Death, phenomena attending, 20, 21, 166
Decomposition, nature of, 6, 91
Dermal gills. See Respiratory Cœca.
Dermis (*δέρμα*, skin), the deep or connective tissue layer of the skin, 326
Descent, doctrine of. See Evolution.
Development, meaning of the term, 43. For development of the various types see under their names
Dextrin, 113
Diastase, 81
Diast'ole (*διαστέλλω*, to separate), the phase of dilatation of a heart, contractile vacuole, &c., 111
DIATOMA'CEÆ (*διατέμνω*, to cut across, because of the division of the shell into two valves), 155 : Figure, 156
Diat'omin, the characteristic yellow colouring matter of diatoms, 154, 155
Dichot'omous (*διχοτομέω*, to cut in two), applied to branching in which the stem divides into two axes of equal value, 318
Differentia'tion (*διαφέρω*, to carry different ways), explained and illustrated, 34, 119
Diges'tion (*διαφέρω*, to arrange or digest), the process by which food is rendered fit for absorption, 12, : intra- and extra-cellular, 229 : contrasted with assimilation, 230
Digest'ive gland, 335, 355, 382
Dimorph'ism, dimorph'ic (*δίς*, twice : *μορφή*, form), existing under two forms, 35, 136, 242, 438, 442
Dioe'cious (*δίς*, twice : *οἶκος*, a dwelling), applied to organisms in which the male and female organs occur in different individuals, 199
DIPH'YES (*δι-φυής*, double) : Figure, 250 : occurrence and general characters, 248 : polymorphism, 249
Diploblast'ic (*διπλόος*, double : *βλαστός*, a bud), two-layered : applied to animals in which the body consists of ectoderm and endoderm, 236 : derivation of diploblastic from unicellular animals, 261
Directive sphere, see also Astrosphere
Disc, Vorticella, 128
Dispersal, means of : in internal parasite, 324 : in fixed organisms, 132, 134
Distal, the end furthest from the point of attachment or organic base, 126
Distribution of food-materials :—in a complex animal, 278 : in a complex plant, 409
Divergence of character, 145
Division of physiological labour, 34
DOGFISH :—Figure, 367 : general characters, 368 : exoskeleton, 369 : endoskeleton (Figures). 372 : enteric canal (Figures), 381 : gills, 383 : blood-system (Figures), 384 : kidney, 396 : gonads, 396 : nervous system and sense organs (Figure), 391 : development (Figure), 397
Dry-rigor, stiffening of protoplasm due to abstraction of water, 21

E

Ecdysis (*ἔκδυσις*, a slipping out), 325
Echinodermata, the, 305
Ect'oderm (*ἐκτός*, outside : *δέρμα*, skin), the outer cell-layer of diploblastic and triploblastic animals, 222, 275
Ect'osarc (*ἐκτός*, outside : *σάρξ*, flesh), the outer layer of protoplasm in the lower unicellular organisms, distinguished by freedom from granules, 4
Egest'ion (*ἐκβέτρο*, to expel), the expulsion of waste matters, 12
Egg-cell. See Ovum.
Elater, 436
Em'bryo (*ἔμβρυον*, an embryo or fœtus), the young of an organism before the commencement of free existence.
Em'bryo-sac. See Megaspore.
Encysta'tion, being enclosed in a cyst (*q.v.*)
End'oderm (*ἔνδον*, within : *δέρμα*, skin), the inner cell-layer of diploblastic and triploblastic animals, 222, 228, 275
Endodermis, 418
End'oderm-lamella, Medusa, 240
Endog'enous (*ἔνδον*, within : *γίγνομαι*, to come into being), arising from within, *e.g.* the roots of vascular plants, 422
Endophragmal System (*ἔνδον*, within : *φράγμα*, protection), 321
Endopodite (*ἔνδον*, within, *πούς*, foot), 323
End'osarc (*ἔνδον*, within : *σάρξ*, flesh), the inner, granular protoplasm of the lower unicellular organisms, 4
Endoskel'eton (*ἔνδον*, within, and *skeleton*, from *σκέλλω*, to dry), the internal skeleton of animals, 372
End'osperm (*ἔνδον*, within : *σπέρμα*, seed), nutrient tissue formed in the megaspore of Phanerogams, 459, 476
Energy, conversion of potential into kinetic, 15 : source of, in chlorophyll-containing organisms, 31

Enter'ic (*ἔντερον*, intestine), **canal**, the entire food-tube from mouth to anus :— Polygordius, 270, 276 : Starfish, 312 : Crayfish, 332 : Mussel, 355 : Dogfish, 381
Ent'eron or **Enteric cavity**, the simple digestive chamber of diploblastic animals. 222
Epiderm'is (*ἐπί* upon : *δέρμα*, the skin) : in animals synonymous with deric epithelium (*q.v.*, under Epithelium) : in vascular plants a single external layer of cells, 416, 420
Epipodite (*ἐπί*, upon : *πούς*, foot), 324
Epi'stoma (*ἐπί*, upon : *στόμα*, month), 321
Epithel'ial cells : columnar, 58 : ciliated, 59
Epithel'ium (*ἐπί*, upon : *θηλή*, the nipple), a cellular membrane bounding a free surface, 244 : **coelomic**, 274 : **deric**, 273 : **enteric**, 274
EQUISE'TUM (*equus*, a horse : *seta*, a bristle) :—Figures, 435, 437 : general characters, 434 : cone and sporophylls, 436 : male and female prothalli, 437 : alternation of generations, 438
Equivocal generation. See Abiogenesis.
EUGLEN'A (*εὐγλήνος*, bright-eyed) :— Figure, 45 : occurrence and general characters, 44 : movements, 44 : structure, 45 : nutrition, 46 : resting stage, 47 : reproduction, 48 : animal or plant ? 180
Euglen'oid movements, 45
Ev'olution (*evolvo*, to roll out), **organic** : definition, 143 : illustration of in connection with species of Zoothamnium (Diagram), 144
Excre'tion (*excerno*, to separate), the separation of waste matters derived from the destructive metabolism of the organism, 16, 281
Exog'enous (*ἐξ*, out of : *γίγνομαι*, to come into being), arising from the exterior, *e.g.* leaves, 422
Exopodite (*ἔξω*, outside : *πούς*, foot), 323
Exoskel'eton (*ἔξω*, outside, and *skeleton*, from *σκέλλω* to dry), the external or skin-skeleton . **cuticular**, 238, 273 : **dermal**, 308, 327, 350, 369
Eye, Crayfish, 342 : Dogfish, 394 :
Eye-spots or **Ocel'li** :— Medusa, 244 : Polygordius, 296
Eye-stalks, 321

F

Fæces (*faex*, dregs), solid excrement, consisting of the undigested portions of the food, 16
Ferm'ent (*fermentum*, yeast, from *fervĕo*, to boil or ferment), a substance which induces **fermenta'tion**, *i.e.* a definite chemical change, in certain substances with which it is brought into contact, without itself undergoing change : **unorganized** and **organized ferments** 80 : **alcoholic**, 76 : **acetous**, 91 : **diastatic** or **amylolytic**, 81 : **lactic**, 91 : **peptonizing** or **proteolytic**, 81 : **putrefactive**, 91 : ferment-cells of Mucor, 168
FERNS :—Figures, 414, 424 : general characters 412 : histology of stem, leaf, and root, 415 : nutrition, 422 : spore-formation, 422 : prothallus and gonads, 425 : development, 426 : alternation of generations, 429
Fertiliza'tion (*fertilis*, bearing fruit) : the process of conjugation of a sperm or sperm-nucleus with an ovum, whereby the latter is rendered capable of development : a special case of conjugation (*q.v.*), 199 : details of process, 260 : in Vaucheria, 173 : in Gymnosperms, 458, in Angiosperms, 475
Filtering air, method of, 99
Fins, Dogfish 369
Fiss'ion (*fissio*, a cleaving), **simple** or **binary**, the division of a mother-cell into two daughter-cells : in Amœba, 19 ; Heteromita, 40 : animal- and plant-cells generally, 65 : Paramœcium, 114 : Vorticella 131
Fission, multiple, the division of a mother cell into numerous daughter-cells :—in Heteromita, 42 : Protomyxa, 51 : Saccharomyces, 74
Fission, process intermediate between simple and multiple, Opalina, 124
Flagellum. See Cilium.
Flag'ellate Infusoria, 107
Flagell'ula (diminutive of *flagellum*), the flagellate germ of one of the lower organisms (often called zoospores, 51, 54
Flagell'um (*flăgellum*, a whip) : defined, 25 : transition to pseudopod. 52, 228
Floral receptacle, the abbreviated axis of an angiospermous flower 464, 471, 473
Flower, a specially modified cone (*q.v.*), having a shortened axis, which bears perianth-leaves as well as sporophylls, 463 : often applied to the cone of Gymnosperms, 452
Food-current, Mussel, 359
Food-vacuole, a temporary space in the protoplasm of a cell containing water and food-particles, 11, 112
Foot : of Mussel, 349 : of phyllula of fern, 427
FORAMINIF'ERA (*forāmen*, a hole : *fero* to bear), 148 : Figures, 149, 150, 151
Fragmenta'tion of the nucleus, 120
Fruit of Angiosperms, 476
Funct'ion (*functio*, a performing), meaning of the term, 9

G

Gam'ete (*γαμέω*, to marry), a conjugating cell, whether of indeterminate or deter-

minate sex :—Heteromita, 41 : Mucor, 156 : Spirogyra, 198 : Vaucheria 173
Gamob'ium (*γάμος*, marriage : *βίος*, life), the sexual generation in organisms exhibiting alternation of generations (*q.v.*) : progressive subordination of, to agamobium in vascular plants, 429, 440, 444, 458, 474
Ganglion (*γάγγλιον*, a tumour), a swelling on a nerve-cord in which nerve-cells are accumulated, 341
Gastric juice (*γαστήρ*, the stomach), properties of, 12
Gastric mill, 334
Gastrolith (*γαστήρ*, stomach : *λίθος*, stone), 334
Gast'rula (diminutive of *γαστήρ*, the stomach), the diploblastic stage of the animal embryo in which there is a digestive cavity with an external opening : characters and Figure of, 295 : contrasted with phyllula, 428
Gemma'tion (*gemma*, a bud). See Budding.
Genera'tion, asexual, See Agamobium.
Generation, sexual. See Gamobium.
Genera'tions, Alternation of. See Alternation of generations.
Generative cell, 455
Generative nucleus, 474
Gen'eralized, meaning of term, 140
Ge'nus (*genus*, a race), generic name, generic characters, 8, 139
Germ-filter, 99
Ger'minal spot, the nucleolus of the ovum, 257
Germina'tion (*germinatio*, a budding), the sprouting of a spore, zygote, or oosperm to form the adult plant : for germination of the various types see under their names.
Gill, an aquatic respiratory organ. 335, 357, 383
Gland (*glans*, an acorn), an organ of secretion (*q.v.*) : gland-cells, 228, 278
Glochid'ium, larva of Mussel, 365
Gon'ad (*γόνος*, offspring, seed), the essential organ of sexual reproduction, whether of indeterminate or determinate sex, *i.e.* an organ producing either undifferentiated gametes, ova, or sperms ; see under the various types, and especially 172, 198, 211, 290
Gon'oduct (*gonad* and *dūco*, to lead), a tube carrying the ova or sperms from the gonad to the exterior, 292
Grapping-lines, Diphyes, 249
Green gland. See Kidney
Growing point : Nitella, 208 : Moss, 403 : Fern, 418 : Gymnosperms, 452
Growth, 13
Guard-cells of stomates, 421
Gullet, the simple food-tube of Infusoria, 47, 110 : or part of the enteric canal the higher animals, 277
GYM'NOSPERMS (*γυμνός*, naked : *σπέρμα* seed) : Figures, 449, 453, 455, 456, 457 ; general characters, 447 : structure and growth of stem, 448 : structure of cones and sporophylls, 452 : reduction of gamobium (prothalli and gonads), 460 : pollination and fertilization, 458 : formation of seed and development of leafy plant, 459
Gynœc'ium (*γυνή*, a female : *οἶκος*, a dwelling), the collective name for the female sporophylls in the flower of Angiosperms, 465, 471

H

Hæm'atochrome (*αἷμα*, blood : *χρῶμα*, colour), a red colouring matter allied to chlorophyll, 26
HÆMATOCOCCUS *αἷμα*, blood : *κόκκος* a berry).—Figure, 24 : general characters, 23 : rate of progression, 23 : ciliary movements, 25, 33 : colouring matters, 26 : motile and stationary phrases, 28 : nutrition, 28 : source of energy, 30 ; reproduction, 35 : dimorphism, 35 : animal or plant ? 180
Hæmoglob'in (*αἷμα*, blood : *globus*, a round body, from the circular red corpuscles of human blood), 58 : properties and functions of, 280
Head-kidney : trochosphere, 297
Heart :—Crayfish, 337 : Mussel, 360 : Dogfish, 384
Heat, evolution of by oxidation of protoplasm, 17
Heat-rigor (*rĭgor*, stiffness), heat-stiffening, 21
Heliotropism, 168
Hepato-pancreas (*ἧπαρ*, liver : *παγκρέας*, sweetbread), 335
Heredity (*hereditas*, heirship), 147
Hermaph'rodite (*ἑρμαφρόδιτος*, from Hermes and Aphrodite). See Monœcious.
Heterogen'esis (*ἕτερος*, different : *γένεσις*, origin), meaning of term, 102 : supposed cases of, 103 : not to be confounded with metamorphosis or with evolution, 104
HETEROMITA (*ἕτερος*, different : *μίτος*, a thread) :— Figure, 38 : occurrence and general characters, 36 : movements, 37 : nutrition, 37 : asexual reproduction, 40 : conjugation, 41 : development and life-history, 42, 43 : animal or plant ? 181
High and **low organisms**, 106
Higher (triploblastic) **animals**, uniformity in general structure of 304
Higher (vascular) **plants**, uniformity in general structure of, 431
Histol'ogy (*ἱστίον*, a thing woven : *λόγος* a discussion), minute or microscopic anatomy, 289

Holophyt'ic (ὅλος, whole : φυτόν, a plant), **nutrition**, defined, 31
Holozo'ic (ὅλος, whole : ζῶον, an animal), **nutrition**, defined, 31
Homogen'esis (ὁμός, the same: γενεσις origin), meaning of the term, 102
Homol'ogous (ὁμόλογος, agreeing), applied to parts which have had a common origin, 242
Homomorph ism homomorph'ic (ὁμός, the same : μορφή, form), existing under a single form, 139
Host, term applied to the organism upon which a parasite preys, 123
HYDRA (ὕδρα, a water-serpent): Figures, 219, 223, 225, 232: occurrence and general characters, 218 : species, 220 : movements, 220: mode of feeding, 221 : microscopic structure, 222 : digestion, 229 : asexual, artificial, and sexual reproduction 230 : development, 233
Hydr'anth (ὕδρα, a water-serpent : ἄνθος, a flower), the nutritive zooid of a hydroid polype, 236
Hydroid (ὕδρα, a water-serpent : εἶδος, form) **Polypes** (πολύπους, many footed), compound organisms, the zooids of which have a general resemblance to Hydra, 234
Hyper'trophy (ὑπέρ, over : τροφή, nourishment), an increase in size beyond the usual limits, 118
Hyph'a (ὑφαίνω, to weave) applied to the separate filaments of a fungus : they may be **mycelial** (see mycelium), **submerged**, or **aerial** : Mucor, 160 : Penicillium, 185
Hyp'odermis (ὑπό, under : δέρμα, skin), Fern, 413, 416
Hypostome (ὑπό, under : στόμα, mouth), 220, 236

I

Immortality, virtual, of lower organisms, 21
Income and **expenditure** of protoplasm, 18
Individual. See Zooid.
Individuation, meaning of the term, 230, 252
Indus'ium (*indusium*, an under-garment, 423
Inflores'cence (*floresco*. to begin to flower), an aggregation of cones or flowers, 454
Infusor'ia (so called because of their frequent occurrence in infusions), 107
Ingesta (*ingĕro*, to put into) and **Egesta** (*egĕro*, to expel), balance of, 32
Ingestion (*ingĕro*, to put into), the taking in of solid food, 11
Insola'tion (*insolo*, to place in the sun), exposure to direct sunlight, 94
Integ'ument (*integumentum*, a covering) of megaspore : Gymnosperms, 456 : Angiosperms, 466
Inter-cellular spaces, 415
Inter-muscular plexus (πλέκω, to twine), 285
Internode (*inter*, between : *nodus*, a knot), the portion of stem intervening between two nodes, 205
Intersti'tial (*interstitium*, a space between) **cells**, Hydra, 224 : **growth**, Spirogyra, 198
Intest'ine (*intestinus*, internal), part of the enteric canal of the higher animals, 277
Intus-suscep'tion (*intus*, into : *suscĭpio*, to take up), addition of new matter to the interior, 13
Iodine, test for starch, 27
Irritabil'ity (*irritabilis*, irritable, the property of responding to an external stimulus, 10

J

Jaws : Crayfish, 324 : Dogfish, 368, 375

K

Karyokines'is (κάρυον, a kernel or nucleus : κίνησις, a movement), indirect nuclear division, 67
Katab'olism (καταβολή, a laying down), 18. See Metabolism, destructive.
Kat'astates (καταστῆναι, to sink down), 18. See Mesostates, katabolic.
Kidney :—Crayfish, 337 : Mussel, 359 : Dogfish, 396

L

Labial palps, Mussel, 355
Larva, the free-living young of an animal in which development is accompanied by a metamorphosis, 293
Larval stages, significance of, Polygordius, 303
Leaf, structure of :—Nitella, 205, 207 : Moss, 403 : Fern, 420 : limited growth of, 211
Leaflet, Nitella, 207
Leg, Crayfish, 324
Lept'othrix (λεπτός, slender : θρίξ, a hair), filamentous condition of Bacillus, 89 : Figure, 87
Leuc'ocyte (λευκός white : κύτος a hollow vessel, cell), a colourless blood corpuscle : —structure of, in various animals (Figures), 57 : ingestion of solid par-

204, 209, 212, 214: occurrence and general characters, 203: microscopic structure, 206: terminal bud, 208: structure and development of gonads, 206, 211: development, 216: alternation of generations, 217
Node (*nodus*, a knot), the portion of a stem which gives rise to leaves, 205
Not'ochord (*νῶτον*, the back: *χορδή*, a string), 377
Nucel'lus (diminutive of *nucleus*, the name formerly applied), 456, 466
Nuclear division, indirect: 64 (Figure)
direct, 67
Nuclear membrane, 63
Nuclear sap, 7, 63
Nuclear spindle, 66
Nucle'olus (diminutive of nucleus), 8, 63
Nu'cleus (*nucleus*, a kernel), minute structure of, 63; Amœba, 7, 8: Paramœcium, 111, 114: Opalina, 121: Vorticella, 128: Nitella, 208, 211: fragmentation of, 120
Nucleus, secondary, of megaspore, Angiosperms, 474
Nutrient solution, artificial, principles of construction of, 77,
Nutrition:—Amœba (holozoic), 11: Hæmatococcus (holophytic), 28: Heteromita (saprophytic), 37: Opalina (type of internal parasite), 123: Mucor 167: Penicillium, 190: Polygordius (type of higher animals), 270, 279: Moss (type of higher plants), 408

O

Ocel'lus (*ὀcellus*, a little eye), structure and functions of, Medusa, 240, 244
Œsoph'agus (*οἰσοφάγος*, the gullet). See Gullet.
Olfactory organ, Crayfish, 342: Mussel, 363: Dogfish, 394
Ommatideum (dim. of *ὄμμα*, eye), 342
Ontog'eny (*ὄντος*, being: *γένεσις*, origin), the development of the individual: a recapitulation of phylogeny (*q.v.*), 146
Oogen'esis (*ὠόν*, an egg: *γένεσις*, origin), the development of an ovum from a primitive sex-cell, 256
Oogon'ium (*ὠόν*, egg: *γόνος*, production), the name usually given to the ovary (*q.v.*) of many of the lower plants.
Oosperm (*ὠόν*, egg: *σπέρμα*, seed), a zygote (*q.v.*), formed by conjugation of the ovum and sperm: a unicellular embryo, 173, 260: origin of nucleus of, 261
Oosphere (*ὠόν*, an egg: *σφαῖρα*, a sphere), a name frequently given to the ovum (*q.v.*) of plants.
Oospore (*ὠόν*, an egg: *σπορά*, a seed), a name frequently applied to the oosperm (*q.v.*) of plants.
OPALIN'A (from its *opalescent* appearance):—Figure, 122: occurrence and general characters, 121: structure and division of nuclei, 121: parasitic nutrition, 123: reproduction, 124: means of dispersal, 124: development, 125
Opt'imum (*optimus*, best) temperature for amœboid movements, 21: for saprophytic monads, 40
Organ (*ὄργανον*, an instrument), a portion of the body set apart for the performance of a particular function, 288
Or'ganism, any living thing, whether animal or plant, 5
Osphradium (*ὀσφραίνομαι*, to smell), 363
Oss'icle (diminutive of *ὀs*, a bone), 308
Ov'ary (*ὄvum*, an egg), the female gonad or ovum-producing organ; see under the various types and especially Vaucheria, 172: atrophy of, in Angiosperms, 474. The name is also incorrectly applied to the venter of the pistil of Angiosperms, 465
Ov'iduct (*ὄvum*, an egg: *duco*, to lead), a tube conveying the ova from the ovary to the exterior, 292
Ov'um (*ὄvum*, an egg), the female or megagamete in its highest state of differentiation: general structure of, 68: minute structure and maturation of, 256; see also under the various types and especially Vaucheria, 173: formation of, in Angiosperms, 474
Ov'ule (diminutive of *ovum*), the name usually applied to the megasporangium (*q.v.*) of Phanerogams.
Oxidation of protoplasm, 15
OXYTRICH'A (*ὀξύς*, sharp: *θρίξ*, a hair), 120 (Figure)

P

Pallium See Mantle.
Palp (*palpo*, to stroke), Crayfish, 325: Mussel, 355
Pancreas (*παγκρέας*, sweetbread), 382
PANDORINA (Figure), 262
Param'ylum (*παρά*, beside: *ἄμυλον*, fine meal, starch), 46
PARAMŒ'CIUM:—Figures, 108, 115: structure, 107: mode of feeding, 112: asexual reproduction, 114: conjugation, 114
Par'asite, parasitism (*παράσιτος*, one who lives at another's table):—Bacteria, 92: Opalina, 123: Mucor, 167
Paren'chyma (*παρέγχυμα*, anything poured in beside, a word originally used to describe the substance of the lungs, liver, and other soft internal organs), applied to the cells of plants the length of