THE ARBORESCENT HABIT IN ANGIOSPERMS

A REVIEW

By

H. BANCROFT

NEW PHYTOLOGIST REPRINT, No. 19

1931
CAMBRIDGE UNIVERSITY PRESS
LONDON: FETTER LANE
E.C.4

PRINTED IN GREAT BRITAIN

CONTENTS

THE ARBORESCENT HABIT IN ANGIOSPERMS

I. Introduction

There has, for a number of years, been much speculation as to the origin and characteristics of Primitive Angiosperms. The chief points under discussion are concerned with:

(1) The ancestral forms from which Primitive Angiosperms may have evolved[1], either mono- or polyphyletically, and

(2) The conditions which favoured their evolution[2].

(3) The habit of Primitive Angiosperms, whether arborescent or herbaceous[3].

(4) Their stem structure, and the presence or absence of a cambium[4].

(5) The form of their leaves[5].

(6) The floral structure of Primitive Angiosperms, whether relatively simple or complex, or whether both conditions were represented; the presence or absence of petals[6]· and the mono- or diclinous organisation of the flower[7][8].

---

[1] Arber and Parkin (8, 9); Parkin (113); Scott (134), pp. 99–102, and (133), Pt. 2, pp. 427–429; Thomas (173, 174, 175, 176); Wieland (189), **2**, 228 *et seq.*, (191).

[2] Sinnott and Bailey (151, 152), see also Berry (17), chap. vi, for the probable physical conditions under which undoubted Angiosperms first appeared in North America.

[3] Compton (40); Eames (47); Hallier (63); Sinnott and Bailey (151); Seward (142); Worsdell (196).

[4] Adkinson (1); Bailey (12, 13); Chrysler (36); Eames (47), Hallier (63); Jeffrey (90, 91, 92); Jeffrey and Torrey (93, 94); Lindinger (106); Sargant (130), Sinnott and Bailey (154); Whitaker (186). See also list of references to anatomical work bearing upon this point given later in the paper.

[5] Sinnott and Bailey (152).

[6] Arber and Parkin (8, 9), Brouwer (29); Campbell (31); Parkin (113); Senn (135); Wernham (185); see also Moss (112), for a review of Modern Systems of Classification, in which are discussed the views of various authors concerning primitive floral states. Papers by Pilger (116), and Vuillemin (182) may be briefly mentioned here, being of interest in reference to primitive types of whole reproductive axes; according to Pilger, the panicled inflorescence is primitive, and the single-flowered axis derived, while Vuillemin believes that the "Amphigonelle," or catkin-like reproductive apparatus, of the Juglandales, Salicales, Cupuliferae and other orders, is the lowest type amongst Dicotyledons.

[7] The hypothetical "Hemiangiosperm" flower of Arber and Parkin (8, 9, 113) is monoclinous; and in the Fossil Cycadophyta so often referred to in connection with the ancestry of Angiosperms, there is evidence that monocliny was the rule amongst the later, more specialised, members of the group (Scott (134), p. 85; Seward (137), **3**, 379, 380, 456–459; Wieland (189), **1**, 139 *et seq.*). Of the older types, *Williamsoniella coronata* and *Wielandiella* were monoclinous (Scott (134), pp. 96, 97), but the *Williamsonia* group as a whole are generally considered—though not proved—to have been diclinous. It is interesting to note, in this connection, that many families of woody Angiosperms represented amongst the earlier fossil-types of the group have diclinous organisation. (See later in the paper.)

[8] Sinnott and Bailey (153).

(7) The type of fruit they possessed.

(8) The number of cotyledons in their embryos[1]; and

(9) The type of their seedling anatomy[2].

These questions cannot be answered by reference to direct and positive evidence. It is not possible to say of any Angiosperm, living or fossil, "This is, or represents, a Primitive Angiosperm." The problems must be attacked indirectly by an impartial consideration of evidence drawn from a consensus of facts; and, in spite of much accumulated evidence, the question of the origin and nature of Primitive Angiosperms is still no more than a matter for speculation.

The question of the habit of Primitive Angiosperms is one which has received much attention, particularly from American botanists. As a result of their studies, chiefly anatomical[3], these workers have concluded that the arborescent habit is primitive for the group, and that the herbaceous habit is derived[4].

This conclusion is opposed to the purely theoretical views expressed, for example, by Campbell, by Coulter and Chamberlain, and by Coulter, Barnes and Cowles.

An evolutionary scheme given by Campbell indicates the suggested derivation of the Angiosperms from eusporangiate heterosporous Filicales ((31), p. 157). This author also remarks on the number of fossil members of the "Amentaceae," and points out that these may have been preceded by herbaceous forms of which there are no traces ((31), p. 229). Coulter and Chamberlain suggest the origin of Monocotyledons from an *Isoëtes*-like ancestor, and that of Dicotyledons from a *Selaginella*-like ancestor, on the ground of similarity of the embryos ((42), p. 287). As an alternative, they suggest a similar

---

[1] Arber (3), chap. vii; see also discussions and references given by Holden and Daniels (83).

[2] For researches and discussions relating to type of seedling anatomy, transition phenomena and their phylogenetic significance, see Arber (2); Compton (39, 40); Davey (43); Hill and de Fraine (75, 76); Holden and Bexon (80); Holden and Chesters (81); Holden and Clarke (82); Lee (101, 102); Sargant (129, 130); Sinnott (148); Tansley and Thomas (165, 166); Thomas (168, 169, 170, 171, 172) See other references given under the section on Seedling Anatomy; and also a report of a discussion on the Vascular Anatomy of Seedlings, at York, 1906, in the *New Phytologist*, **5**, 1906, 182.

[3] Bailey (10, 11, 12, 13); Bailey and Sinnott (15); Eames (46); Flint (50); Hemenway (64); Hoar (77); Holden (84, 85); Sinnott (145); Sinnott and Bailey (150, 152); Thompson (177); Torrey (181); Whitaker (187, 188). See also the list of references on p. 1, footnote 4; and a review of the earlier papers dealing with these anatomical studies, by Tansley (163).

[4] Eames and MacDaniels (47), chap. xi, pp. 245–248; Jeffrey (92), chaps. xiii, xxviii; Sinnott (149), chap. vi, pp. 101–104.

view to that held by Campbell. Coulter, Barnes and Cowles indicate that "trees are a recent development" ((41), p. 738), an adaptation to ecological conditions. These views imply, to a greater or less extent, the primitiveness of herbaceous forms.

It is proposed, in the present communication, to review the available evidence concerning the habit of Primitive Angiosperms.

II. SUGGESTIONS FROM THE HISTORY OF OTHER PHYLA

Comparisons with regard to habit have been drawn between Angiosperms and other groups of which we know a part, at least, of the history from a study of fossil types (cf. Bailey(12), p. 235; Eames(47), p. 215; Sinnott and Bailey(151), pp. 549–550).

Before embarking upon these comparisons, however, it will be well to remember Professor Seward's dictum that "the study of the fossil record raises more problems than it solves" ((141), p. 597), and therefore to treat its evidence tentatively and cautiously.

The oldest members of the Equisetales at present known were arborescent, with well-marked cambial activity and considerable secondary growth; the geological record from Palaeozoic through Mesozoic to recent times, shows the gradual diminution in size of the individuals, the present-day Equiseta being herbaceous and typically without secondary growth, or with only a small amount of cambial activity at the nodes. The evidence, at first sight, seems to point in this instance to the derivation of the herbaceous from the arborescent type, by a process, as Jeffrey and Torrey suggest, of degeneration, manifested in the loss of cambial activity ((94), p. 246).

Further, the majority at least of the oldest known Lycopods were trees, and the present-day types are herbaceous. It has been suggested that the Triassic genus *Pleuromeia* may be a reduced intermediate form, linking the living herbaceous *Isoëtes* with the arborescent Carboniferous plants[1].

The evidence, then, in these two phyla, according to Eames, seems to favour the primitiveness of the woody, and the derivation of the herbaceous habit, the survival of the latter, as this author believes, being probably "due to an adjustment to modern conditions, involving the loss of secondary growth and the acquisition of a low or prostrate habit" ((47), p. 215).

---

[1] Seward(137), **2**, 72; see, however, Scott ((133), Pt. 2, p. 403), who remarks on the difficulty in accepting this suggestion, if, as is stated, the sporangia occurred on the underside of the sporophylls in *Pleuromeia*.

In the case of the Lycopodiales, however, herbaceous and arborescent forms are known to have occurred side by side in the Carboniferous; *Miadesmia*, for example (16), was herbaceous, though it was obviously a specialised plant, and cannot be taken as representative of the Lycopod flora of the time. But various other small and apparently more normal non-woody plants have been referred to the genera *Lycopodites* and *Selaginellites* in the same group[1]; and since these herbaceous forms were contemporaneous with the arborescent Lycopods, it is impossible to say from any direct evidence which represents the more primitive condition for the group. In any case, as Halle has pointed out (61), the modern herbaceous Lycopods are more likely to be the direct descendants of the former, than to be degeneration products of the latter types.

There may, moreover, have been more of the herbaceous forms than are known, for woody plants are much more likely to be preserved as fossils than delicate herbaceous plants; so that the overwhelming majority of woody plants in the geological record of the Equisetales and Lycopodiales does not mean, necessarily, that non-woody forms were few in number in the early history of these groups.

It is debatable to what extent a comparison between the Equisetales and the Lycopodiales on the one hand and the Angiosperms on the other, is valid in the absence of sure evidence concerning the actual origins of the groups under consideration, and the physiological conditions under which they developed. The beginning of the phytological record shows the arborescent types of the Equisetales and Lycopodiales well established and highly developed. Their origin and ancestry are not known, and there is nothing to indicate the habit of the first members of these two phyla, or that of their immediate predecessors[2]. A belief in the algal ancestry of vascular

---

[1] Seward (137), **2**, 73–88. Note also that *Lepidodendron Harcourtii* is not yet known with secondary thickening; it may, however, be merely a non-thickened portion of a larger form (Scott (133), Pt. 1, p. 124).

[2] It is questionable how far the early Devonian "herbaceous" Psilophytales may be considered as the predecessors of any one group They certainly show a simple organisation, and are so far synthetic in character, that the members of the Rhyniaceae have been variously referred to the Pteridophyta (Kidston and Lang (95), Pt. 1, p. 779; Scott (134), p. 191), and to the Thallophyta (Arber (7), p. 72). Comparisons have also been made between the Rhyniaceae and the Bryophyta (see Campbell (32), pp. 7, 8; and cf. Halle's *Sporogonites* (62), with Kidston and Lang's *Hornea Lignieri* (95), Pt. 2, pp. 611–616, plates 4–10); while Bugnon (30) proposes an entirely new group, "Thalloxylophyta," for the reception of undifferentiated types with a partly developed vascular system, standing in an ancestral relationship to the Bryophyta and Pteridophyta—or,

plants is, however, general[1], and in view of the typically non-vascular nature of the Algae, it seems reasonable to suppose that, if the evolution of land plants from simple types took place actually on land,

---

at any rate, "acting as synthetic links" between the two groups (Bower(25), p. 9). At the same time, as Scott points out, it is not certain whether the simplicity of the Rhyniaceae is really an index of primitiveness, for its peat habitat was a specialised one, and the members of the family may represent the reduction products of some algal stock; moreover, the allied genus *Asteroxylon*, also from the Rhynie Chert-beds, had a much more advanced organisation, similar to that of a Lycopod and showing resemblances to the Psilotaceae, and to the Ferns also, if the assignation of reproductive structures is correct (Scott(134), pp. 191–195).

[1] Although the algal ancestry of vascular plants is generally conceded, there is considerable diversity of opinion concerning the *manner* of their evolution. According to some writers, vascular land plants evolved from simple forms on the land itself, producing the organisation suited to land conditions (Bower(24), p 3; Fritsch(52), (53), p. 186; Lignier(105); Potonié(117)). Church(37), on the other hand, without reference to fossil evidence, holds that land plants arose from already highly organised transmigrant Algae, which had evolved from the free-swimming organisms ("Plankton") of a universal ocean, through the "Phytobenthon" stage of *rooted* plants, which succeeded to the Plankton stage as the sea-bottom began to rise. These rooted plants reached a considerable degree of organisation, so that, as the land emerged from the sea, it bore an already highly differentiated flora Two objections to Church's contentions may be pointed out: a geological objection to the postulation of a "universal ocean"; and a biological objection to the possibility of highly developed plants adapting themselves to new, land, conditions.

Diversity of opinion also centres around the question of the mono- or polyphyletic origin of vascular plants. Halle((62), p. 39) upholds the view of their monophyletic origin from an ancestral group of vascular plants. Kidston and Lang, while generally in agreement with Halle, think that the evidence as to the origin of vascular plants is insufficient to allow of definite conclusions ((95), Pt. 3, p 673; and Pt. 4, p. 843); these authors also suggest "the convergence of Pteridophyta and Bryophyta backwards towards an Algal stock" ((95), Pt. 3, p. 675), a view approaching that of Lignier(103, 104), who referred Pteridophyta and Bryophyta to an ancestral terrestrial group, the "Prohepatics"

Church is emphatically in favour of the polyphyletic origin of vascular plants, for he holds that all the main lines of the land flora were already differentiated in the benthic stage, having had independent origins even as far back as the unicellular (plankton) phase ((37), p. 41) Seward, in his Hooker Lecture of 1922 ((139), pp. 237, 238), made a suggestion of polyphyletic origins even more extreme than that proposed by Church In referring to the difference in type between Palaeozoic and Mesozoic Ferns, he suggested that transmigration may have been a recurrent, instead of a single, process. So that "it is conceivable that plant-life viewed as a whole may best be represented by separate and independent lines of evolution, or disconnected chains which were never united, each being initiated by some revolution in the organised world" Arber ((7), pp. 72–87), following in general the ideas of Potonié(117, 118, 119), also believed in the separate origin of the four main Pteridophytic lines (Sphenopsida, Lycopsida, Pteropsida and Psilotales) from algal stocks; interesting in comparison with Seward's suggestion, quoted above, is Arber's view that the Psilotales evolved from the Algae much later than the other groups "possibly in Mesozoic times or even later" ((7), p. 87). Scott ((134), p. 202) concedes that the theory of polyphyletic origins of the main groups of vascular plants "Lycopsida, Articulatae (= Sphenopsida), Ferns, and perhaps the first *vascular* land plants were at least not arborescent[1]; and in this connection may be mentioned the opinion of Dr Scott, expressed in his Presidential Address to the Linnean Society in 1909, that cambial growth was at first most likely absent in the history of vascular plants[2]. How far the Carboniferous Equisetales and the Devonian and Carboniferous Lycopodiales were removed from the first vascular plants, it is impossible to say; but it is conceivable that when vascular plants first evolved, the inherent vigour of the new group or groups led not only to rapid increase in the *number* of individuals, but also to a rapid increase in the *size* of the individuals, along one or more lines of development. The group or groups as a whole, and the various lines within the groups might, therefore, comparatively soon be represented by a large number of woody plants. In course of time, it may be supposed, a zenith of development was reached; subsequently, those members of any line which had attained great complexity and had thereby lost their plasticity, were unable to adapt themselves to any change of ecological conditions which might come upon them, and they, in consequence, died out. Other arborescent types, more adaptable, may have given rise to less woody types by reduction[3]; and thus the group slowly declined, coming to be represented only by the originally smaller and less

---

the seed plants, is evidently quite tenable," though, in the present state of our knowledge, "we cannot be certain that there may not have been a common initial group of vascular plants, from which all the later lines diverged." He concludes (pp. 204, 205) that the "question of the single or multiple origin of the races of vascular plants must still be left open," because it is impossible to determine whether the various similarities of structure and reproduction in the main groups are due to affinity, or to "a like response to like conditions." (See also Scott (132).)

[1] Cf. one of the letters of the late Professor H. H W. Pearson to Professor Seward, in which he stated his belief that "the first vascular plants must have been herbaceous" (Seward (138), p. v).

[2] Scott (131), pp. 9 and 10: "It is an interesting question whether there was ever a time without it" (i.e. secondary thickening). "Was the power of cambial growth at some period or other, however remote, a new acquisition, or is it as old as the vascular tissues themselves?...Widely spread as it was, the evidence on the whole points to cambial growth having been a secondary acquisition in the history of the race as in that of the individual plant....The argument rests on the relatively great development of the *primary* vascular tissues in many Palaeozoic plants, on the frequent sharp distinction between primary and secondary formations, and on the late appearance of the latter in individual development." (See, however, the proposition advanced by Church, to which reference is made on p. 7.)

[3] Cf. Tansley ((162), p. 131), who states that there is "a great primary tendency to increase in bulk and complexity", and that subsequently competition leads to limitation, or a considerable reduction in size and complexity; see also Eames (47), p. 215. Jeffrey and Torrey ((94), p. 246) refer to the Vascular Cryptogams as being represented in the living flora by "degenerate" herbs, cambial activity having ceased.

complicated forms, and by reduced forms, the descendants of arborescent types[1] (Diagram 1).

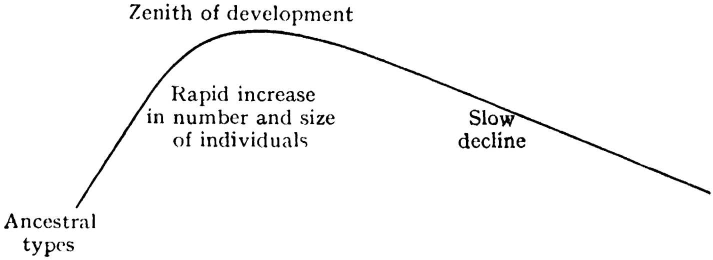

Diagram 1. The course of evolution of plant groups (e.g. Equisetales or Lycopodiales), according to the proposition outlined above. The Lower Coal-Measure Age probably marks the "zenith of development" of the Equisetales; that of the Lycopodiales was perhaps a little later.

It is evident, then, from the foregoing considerations, that ultimate primitiveness of the arborescent habit cannot safely be assumed for the Equisetales and Lycopodiales; and, in such case, a comparison of the Angiosperms with them in this respect is unlikely to produce data of any value.

It is necessary, however, to keep in mind Dr Church's suggestions, made independently of fossil evidence, that evolution of the various plant phyla may have taken place in the sea itself (see footnote 1, p. 5). According to this view, certain members of the marine "phytobenthon" giving rise to the land flora may have already possessed the arborescent habit, as in the recent genus *Lessonia*, or a shrubby habit, as in *Cystoseira* and *Sargassum* ((37), p. 24); in such Laminarian and Fucoid types, with their secondary growth from a meristematic tissue, "the essential features of a modern woody stem are immediately foreshadowed" ((37), p. 37). Further, "It is to the more massive, more resistant, self-supporting perennial stocks of marine phytobenthon, with massive crampon-attachment, large and active photosynthetic area, that one must look for the greater possibility of somatic adaptation to the new necessities of the problem; and so far, it will be among the higher Fucoids (*Sargassum*, *Turbinaria*) and Laminarians that analogies may be sought for the factors making for success in the first land-types of true Land-Flora" ((37), pp. 36, 37).

---

[1] Amongst animal phyla, the Reptilia as a whole, and also the Cephalopoda, show a notable parallelism with this scheme in their rapid development and comparatively slow decline. The same scheme also applies to the number, at least, of types and individuals in the Cycadophyta and Ginkgoales amongst other plant phyla (cf. Wieland (190), p. 404, and Diagram 2, p. 401).

Church emphasises the fact that land plants cannot have "been evolved from Laminarians, but the latter may present a clue to the evolution of the mechanism" of secondary growth ((37), p. 83, footnote 1); and in this connection, it is interesting to note that Scott, while on the whole in favour of the secondary acquisition of cambial growth in land plants, admits the possibility of its having existed even amongst the earliest types, an admission to which he is led by the occurrence of secondary growth in present-day sea-weeds ((131), p. 10). It should be remembered here, that the fossil *Nematophyton* (= *Nematophycus*), referred to the Algae and compared with the gigantic marine sea-weeds of the present day, occurred in the Rhynie peat-beds with *Rhynia* and other members of the Psilophytales ((95), Pt. 5, p. 882); the association of this plant "with vascular land-plants in an inland locality suggests an unexpected degree of adaptability in the higher Algae of those days," as Scott points out ((134), p. 197). Church does not accept *Nematophyton* as a Laminarian ((37), p. 49), but if, as seems likely, it was truly an Alga, it may have been a Chlorophycean type; and if so, it may provide an even better clue to the development of terrestrial plants than the Laminarians themselves.

According to these suggestions, therefore, some at least, of the first true land plants may have been arborescent, with secondary growth; and the main Angiospermous line itself may have included woody types at its initiation, although in Angiosperms, "no direct evidence of the older epochs remains" ((37), p. 84).

Turning to other plant groups in passing, it is interesting to note that the Gymnosperms (including Pteridosperms), well-developed in Carboniferous and even in Devonian times, were, and still are, characteristically woody with well-marked secondary growth. This group, like the Equisetales and Lycopodiales, at first sight appears to support the idea of the primitiveness of the arborescent habit and of secondary growth, these characters having in the main persisted[1], particularly in the Coniferales—which are, of course, the successful Gymnosperms of the present day—without giving rise to any herbaceous types (see Sinnott and Bailey (151), p. 562). But here, again, the pre-Devonian history of the group is not known; and even if the Pteridosperms are regarded as representing primitive Gymnosperms, they are known only as contemporaneous with more highly

---

[1] Exceptions occur in the case of small Cycad types and members of the Gnetales; these however show, particularly in the latter case, adaptations to extremely specialised conditions.

developed members of the group, with which they possessed in common the power of secondary growth.

The Ferns, on the other hand, are known from Upper Devonian times onwards as a group in which cambial activity producing secondary growth never became established (Scott (131), p. 9), though it appears in various species of the recent genus *Botrychium*, in *Botrychioxylon* and *Metaclepsydropsis* amongst Palaeozoic ferns, and in *Osmundites Kidstoni* of Mesozoic times. It is significant that the later and more advanced ferns do not show secondary growth, although some of them (members of the Cyatheaceae), like some of the Palaeozoic types (Psaronieae), have assumed tree-like proportions without it (Bower (27), p. 294)[1]. It rather appears that a *capacity* for secondary growth was present in the early ferns, but that cambial activity was soon abandoned, in contrast with its retention in the Gymnosperms. But still there is no indication, from fossil evidence, that the ancestry of the Filicales was arborescent.

The Gymnosperms and Filicales, then, are no more productive of decisive evidence, either one way or the other, than the two phyla at first discussed.

III. EVIDENCE FROM THE FOSSIL RECORD OF THE ANGIOSPERMS, AND PHYLOGENETIC CONSIDERATIONS

Although it appears doubtful whether the tree habit is primitive for vascular plants as a whole, the possibility of its primitiveness for the Angiosperms themselves is not precluded. Attention must therefore be turned to the fossil record of the Angiosperms, and to phylogenetic considerations.

Until recently, knowledge of the fossil record of the Angiosperms has indicated that they appeared suddenly in Lower Cretaceous times, and that by the Upper Cretaceous, many Angiosperms representative of Dicotyledons as a whole, together with some Monocotyledons, were in existence[2].

Newer work, however, is pushing the Angiosperm record further back. Simple ovate leaves (*Phyllites*) have been recorded by Professor Seward from the Stonesfield Slate of Jurassic age ((136), p. 152, Pl. XI); their appearance certainly suggests Dicotyledonous affinities, but it is not possible as yet to refer them more definitely to any systematic position.

---

[1] Cf. the Palms, amongst the typically herbaceous Monocotyledons.

[2] Scott (134), pp. 42–56. See types given by Berry (17); Knowlton (96), pp. 142–170; Stopes (160); Stopes and Fujii (161). Note also Guppy's suggestion, in reference to Angiosperm evolution, that there was an "era of origination"

Dr Hamshaw Thomas has recently described some undoubtedly "Angiospermous" fruits with enclosed seeds, and some stamens, from the Inferior Oolite (173, 174, 176); these are therefore of a greater age than *Phyllites*. The fruits are referred to the new genera *Gristhorpia* and *Caytonia*, and the stamens to the old genus *Antholithus*, while the new group "Caytoniales" is proposed for their reception; it is further suggested that the leaves long known as *Sagenopteris* may belong to these plants[1].

The Caytoniales are thus the oldest "Angiospermous" group so far recorded, for Hoskins' "stem," *Angiospermophyton*, of Palaeozoic age (86), cannot be accepted as an Angiospermous type[2].

Nothing appears to be known as to the habit of these very old Angiosperms. The vast majority of types recorded from both the Lower and Upper Cretaceous rocks, however, are woody, e.g. *Woburnia porosa*[3], one of the oldest species, from the Lower Cretaceous (Lower Greensand) of Bedfordshire, and *Jugloxylon*, *Fagoxylon* and others[4], from the Upper Cretaceous of Japan; while herbaceous types, e.g. grasses and sedges, increase in number in the younger strata ((96), pp. 165, 172). Thus, on direct evidence alone, it would appear that the arborescent habit is the older in the Angiosperms. But, as is well realised, the imperfections of the fossil record render it incapable of supplying trustworthy data on such a point.

Many speculations as to the immediate ancestry of the Angiosperms, however, reveal a prevailing idea that they are related to woody types such as those of the Cycadophyte alliance[5]. Arber and Parkin, in 1907 and 1908, suggested a relationship between the Angiosperms and the Gnetales through Ranalean types, the whole alliance having arisen from a hypothetical Mesozoic group[6]; this

and an "era of differentiation" ((59), pp. 161, 471); since Angiosperms were well differentiated by the Upper Cretaceous, the period of origination must have been considerably earlier. (Cf. Wieland's suggestions (190), p. 401, Diagram 2; and (193))

[1] Thomas (174), pp. 331–340. Note that Berry (18) recommends caution in accepting both the angiospermous nature of the Caytoniales, and also their relationship with *Sagenopteris*.

[2] See Seward (140) who believes this supposed monocotyledonous stem to be a medullosean petiole.

[3] Stopes (160), p. 92, Pl. 7, fig. 7, and Pl 8, fig. 8. *W. porosa* is a type recalling the structure of the tropical Dipterocarps.

[4] Stopes and Fujii (161), pp. 62, 64; Pl. 7, fig. 48, and Pl. 8, figs. 50–53. See also Berry (17) and Knowlton (96) for Cretaceous Angiosperms.

[5] Arber and Parkin (8, 9); Parkin (113); Wieland (189, 190, 191). See also Carpentier (33).

[6] This suggestion was made with reference to the reproductive structures, and it is noteworthy that the stamens, at least, of the hypothetical "Hemiangiosperm" flower agree very closely with those of the subsequently described

group—the "Hemiangiospermae"—Arber and Parkin included amongst the Cycadophyta. Parkin, in 1923 (113), restated this theory before the Linnean Society, and has since (114) shown a similarity of stomatal structure in Ranalean, Gnetalean and Bennettitalean types, which, he contends, is significant from the standpoint of the phylogeny of the Angiosperms.

The extension of the Angiosperm record into Jurassic strata makes it difficult to regard any group of Mesozoic Cycadophyta as ancestral to the Angiosperms, though, as Wieland suggested and maintains, the Angiosperms and the known Cycadeoids may have come from a common stock, the two groups going far back geologically ((189, 191); cf. Scott (134), p. 102). But the later Cycadeoid flowers, at least, show a specialisation comparable with that of the more advanced Angiospermous flowers (192); the Gnetales, associated by Arber and Parkin with the Angiosperms in a community of origin from types of a Cycadophyte relationship, are specialised and unusual forms, and nothing is definitely known concerning their fossil history; the Ranales, so often referred to as a basal type amongst Angiosperms, show a wide range of habit, including trees, shrubs and herbs, the latter having probably arisen in response to special, geophytic conditions. Such considerations increase the difficulty of determining what may have been the prevailing habit of the ancestral stock of Angiosperms.

Dr Hamshaw Thomas's researches on the Caytoniales have led him farther back than Mesozoic times for the origin of the Angiosperms. In 1921, he pointed out that the Caytoniales may be a link between Pteridosperms and modern Angiosperms (173), and in 1925, he further suggested that *Glossopteris*, a probable Pteridosperm of the Carboniferous flora[1], may perhaps represent the stock from which both the Caytoniales and the modern Angiosperms were derived ((174), pp. 353–354; (175)); this suggestion is based upon the similarity of the *Sagenopteris* leaves, associated with members of the Caytoniales, to those of the *Glossopteris* type. Little is definitely known of the habit and structure of members of the *Glossopteris*

Williamsonia mexicana of Wieland (cf. Scott (134), pp. 92, 93). Thompson (178), on anatomical grounds, suggested a relationship between the Angiosperms and the Gnetales, though he believed the Gymnospermous affinities of the Gnetales to be with the Conifers rather than with the Cycadophyta. Thompson's later work, however, leads him to prefer a view of parallel evolution of the vascular structures of the Angiosperms and the Gnetales (179, 180).

[1] Cf. Walkom (183), who has described a seed, *Nummulospermum bowenense*, associated with the leaves of *Glossopteris*, in the Permian of Queensland, thus indicating the Pteridosperm nature of *Glossopteris*.

flora, though *Glossopteris* itself appears to have been low-growing, with a creeping stem; and if this alliance does indeed include the ancestral Angiosperm stock, enquiries from this source, also, are somewhat barren so far as the habit of Primitive Angiosperms is concerned[1].

It appears, therefore, that the fossil record of the Angiosperms themselves, and any speculations as to the origin of the group, do not help greatly towards a knowledge of its primitive habit.

IV. EVIDENCE FROM THE GEOGRAPHICAL DISTRIBUTION OF THE ANGIOSPERMS

Some evidence as to the relative antiquity of herbs and woody plants may be sought in a study of the present geographical distribution of the two types.

As Sinnott and Bailey have shown (151), the vegetation of the cooler regions of the globe is largely herbaceous, while that of the warmer areas is largely composed of woody plants; the climate of these warmer regions, according to Sinnott and Bailey, probably more nearly approaches that under which Angiosperms, as a group, first appeared[2].

Further, as these authors point out, land areas which have long been isolated must possess a flora which is very ancient, especially so far as the endemic forms are concerned; and it has been found that in the continental areas of the Southern Hemisphere, and in isolated islands, the most ancient members of the vegetation—that is, the

---

[1] At a meeting of the Linnean Society on January 21st, 1926 (176), a more detailed suggestion as to the immediate relationships of the Caytoniales was made by Dr Hamshaw Thomas, namely, that though it is unlikely that they "represent the direct ancestors of the flowering plants" (p. 22), there may have existed, in Mesozoic times, a group of plants derived from Pteridosperms which resembled the Caytoniales in the structure of their sporophylls, and the Bennettitales in the strobilar arrangement of the sporophylls. "From such a group, many of the modern flowering plants may have been derived" (pp. 24, 25). The seed structure of *Caytonia* indicates a relationship with the Bennettitales, even though "somewhat distant"; this fact and the foregoing suggestion again link the Bennettitales with Angiosperm ancestors, probably through a common group of Pteridosperms. Berry (18), while cautious in accepting Thomas's conclusions, points out that if they "are correct, then these Middle Jurassic plants help bridge the gap between Gymnosperms and Angiosperms, and introduce us to a type which combines fern-like foliage, and gymnospermous seeds enclosed in angiospermous carpels."

[2] Sinnott and Bailey ((152), p. 17) state that it has generally been taken for granted that the Angiosperms came into being under a *tropical* environment; they claim, however, that the group must have had its origin "in a climate, which though doubtless very equable and devoid of extremes of temperature, was essentially a temperature one. Such a climate, so far as we are able to judge of conditions in the Mesozoic, could only obtain, as a general rule, in

species of endemic genera—are overwhelmingly woody; while the more recent members—the non-endemic species—are mainly herbaceous[1]. Sinnott and Bailey note that the *annual* herb, in particular, is generally lacking in isolated insular floras[2].

These facts, the authors conclude, indicate that the original Angiospermous flora of the world was for the most part, at least, composed of woody plants. The development of herbs, they suggest, was perhaps due in great measure to the progressive refrigeration of the climate during the course of the Tertiary era; and it seems to them not improbable that a large number of herbaceous types were developed on the mountains of the great land mass of what is now the North Temperate Zone; that is to say, they were developed where refrigeration would be likely first to occur. Cooler conditions may have been effective in gradually and progressively stunting woody plants, until their aerial portions persisted only for a single growing season, and until, finally, the annual herb was produced ((151), pp. 597–599; see also Sinnott (147)).

If there is truth in Dr Hamshaw Thomas's suggestions as to the ancestry of Angiosperms amongst the *Glossopteris* alliance, the above considerations indicate a possible origin of herbs actually amongst the ancestral types of the modern group; for the dominant plants of the Permo-Carboniferous *Glossopteris* (or *Gangamopteris*) flora were apparently reduced in size as compared with the dominant plants of the immediately preceding Carboniferous flora, and the change in the type of flora coincided in time and distribution with widespread and severe glaciation and refrigeration affecting a large southern land area, known as Gondwana Land[3].

Herbs, with their short life cycle, are able to survive periods of cold underground or in the form of seeds, and having thus developed and become adapted to adverse conditions, they are "the most hardy and aggressive types of vegetation, and have consequently been able to invade successfully all regions of the globe" ((151), p. 596). In those families, of course, where trees and shrubs have been able to endure the cold, few or no herbs have been produced; this may

---

upland or mountainous regions." Since fossilisation in such regions would be rare, this suggestion is in accordance with the fact that comparatively few Mesozoic Angiosperms are known.

[1] Cf. Wallace, who remarks on the shrubby nature of endemic genera in the Hawaiian flora, these genera being represented elsewhere largely by herbs; he also notes the occurrence of "many strange arborescent Compositae, as in other oceanic islands" ((184), pp. 323–328).

[2] A criticism, by Mrs Arber, of this point is given later (p. 16).

[3] See Knowlton ((96), pp. 103–109), for a summary of Permo-Carboniferous conditions, and of the flora of this period; also Seward (143).

have been the case in the Salicaceae, Betulaceae, Fagaceae, Rhamnaceae, Tiliaceae and other families.

Under adverse climatic conditions, herbaceous forms may also have been evolved in mountainous regions in the tropics, and in the Southern Hemisphere. Of considerable interest in this connection are Professor Small's speculations concerning the origin and development of the Compositae, a family composed chiefly of herbaceous species ((155), chap. xi); he gives a sketch of the transformation of a tropical arborescent Lobelioid type, *Siphocampylus*, into an Andean Composite species with all the essential characters of a *Senecio*, a genus including plants of very various habit, although, in this country, it is typically represented by herbs. Considering the Andes as a point of origin and dispersal of the Compositae, it is significant to note the number of species of the family recorded for this region by the explorer, Richard Spruce, and also his observations as to their distribution; for example, he says "from the mouth of the Amazon to the cataracts of the Orinoco and the foot of the Andes, with the exception of a few scandent Vernoniae and Mikaniae, and of a few herbs on inundated beaches of the rivers, the species of Compositae that exist are weeds, common to many parts of tropical America, nor did I meet with more than one arborescent Composita (*Vernonia polycephala* DC.) in the whole of that immense area. But in ascending the Andes, from 1200 feet upwards, Compositae increase in number and variety at every step, and include many arborescent species" ((158), **2**, 288).

Many plants, particularly in the tropics, may have become herbaceous or semi-herbaceous through the assumption of the climbing habit, as in the Asclepiadaceae, Cucurbitaceae, Vitaceae and other families; and here again, Spruce's observations on the Andean Compositae are interesting, for amongst the shrubby and arborescent types of the higher altitudes, he also notes woody twiners, chiefly Senecionidae, and twiners of a more herbaceous type belonging to the Mikaniae ((158), p. 288).

With regard to tropical lowland herbs, many have, no doubt come down from the mountain areas—as, very probably, in the case of the Compositae of the Amazon; others have perhaps been evolved under tropical conditions as a result of alternating wet and dry seasons. Discontinuity in the amount of available moisture seems to have been the controlling factor in the production of herbs in desert and the drier regions generally; as Dr Willis notes, in his studies on geographical distribution, "So long as there is a reasonable amount of rainfall, not too much concentrated into one period of the year, the usual type of covering of the soil in countries that have not been disturbed by ice-periods, or by man, is forest"; and the general effect of climatic change, caused for example, by the development of a chain of mountains "transverse to the prevailing damp wind, is to encourage the growth upon the lee side of herbaceous and shrubby plants which can stand greater extremes of drought"((195), pp. 42, 43). While Sinnott and Bailey ((151), p. 595) are of the opinion that "the great mass of herbaceous vegetation" is of comparatively recent origin, they concede that it is "altogether probable that dicotyledonous herbs were developed in rare instances in the Cretaceous or very early Tertiary[1]," where they were exposed to local xerophytic conditions. Here, again, it may be pointed out that if herbs were developed under xerophytic conditions in Cretaceous or Eocene times, it is reasonable to suggest a still earlier inception of the herbaceous habit, in Angiosperms, namely, amongst the very first members of the group[2]—or, it may be, amongst their immediate ancestry in some differentiation period[3]—as a result of the arid, desert conditions of Triassic times, conditions which were possibly also effective in the reduction in size and woodiness of certain Equisetalean and Lycopodialean types.

Therefore, while the present geographical and climatic distribution of the Angiosperms may point, at first sight, to the comparatively recent development of many herbaceous types, there is no reason to believe that the earliest members of the group were exclusively woody. Opinions recently advanced by Mrs Arber (6), indeed, are definitely opposed to the view that any of them were woody. With regard to this question of geographical distribution, Mrs Arber quotes de Candolle's list of the most widely distributed flowering plants; each member of the list is a herb, and the indications are, therefore, that trees tend to be more restricted in distribution than herbs. Applying Willis's "Law of Age and Area," Mrs Arber suggests that this tendency broadly indicates the greater antiquity of herbs amongst the Angiosperms, though, as she admits, Willis himself (194) "has disclaimed the application of this theory to the problem of the relative age of trees and herbs" ((6), p. 73).

---

[1] Note that the Andes were developed in Cretaceous times, and Small ((155), chaps. xi, xii, xiv) suggests the origin and development of the Compositae in this area in the late Cretaceous or early Eocene.

[2] Note that Willis, in considering the factors which favour or inhibit the dispersal of species, comments on the possibility that herbaceous types may be very ancient, but restricted in distribution until new physical conditions favoured their dispersal ((195), p. 48).

[3] See p. 9, footnote 2; see also Wieland (190), Diagram 2, p. 401, and (193); Sinnott and Bailey (152), p. 17.

The lack of annual herbs in isolated insular floras, quoted by Sinnott and Bailey in support of their view of the derived nature of herbs (see p. 13), is explained by Mrs Arber as follows. A single unfavourable season may so hinder the setting of seed, that "a whole batch of immigrant annuals" may be exterminated at once. It is therefore more difficult for annuals to become established than for perennials, which are not dependent for continuance upon the seed of a single season. Further, Mrs Arber points out that isolated insular floras referred to in the literature are nearly always in the warmer and moister parts of the world, where the growth of woody plants is so favoured that they would tend to crowd out smaller plants such as annual herbs.

Finally, it must be borne in mind that speculations—such as those quoted in the foregoing pages—concerning the climatic conditions of previous ages and their possible effect on vegetation, do not necessarily greatly contribute to a solution of the problem of habit-evolution in the Angiosperms; for, as Professor Seward has recently maintained, a correlation of present-day plant type and climate may not be taken too definitely as an index to the correlation of plant type and climate of other ages; in the course of time, plants may have changed "in their susceptibility to external factors"; and "we are not entitled to attribute to extinct and recent alike the same constitutional qualities" ((143), p. 214).

V. EVIDENCE FROM THE STRUCTURE OF THE ANGIOSPERMS

(1) *Seedling anatomy*

Much attention has been given, both in this country and in France, to seedling anatomy, one of the chief aims of the researches being phylogenetic. While "there is a remarkable uniformity in the main features of seedling anatomy, particularly as displayed in the hypocotyledonary region[1]," phylogenetic conclusions appear at present to be somewhat conflicting. Diversity of opinion centres round three points:

(1) Whether seedling anatomy may be used profitably in deducing the phylogeny of the Angiosperms[2].

(2) Which type of seedling root structure, diarch or tetrarch, is

---

[1] Thomas (172), p. 448. See also Sinnott (148), whose seedling studies lead him to regard the cotyledonary node as being very uniform in structure throughout large groups.

[2] Cf. the negative views of de Fraine (45), Hill and de Fraine (75, 76), Lee (102) and Smith (156), with those expressed by Arber (2), Compton (40), Fritsch (51), Sargant (129, 130), Tansley and Thomas (165, 166), and Thomas (168, 169).

the more primitive[1]. These two questions, of course, lead up to the main question under consideration here, namely,

(3) What may be the primitive habit of the Angiosperms as deduced from seedling structure[2].

Professor Compton, in his comprehensive researches on the seedling anatomy of the Leguminosae, points out that: "From the standpoint of phylogeny, as well as that of the better comprehension of anatomy, it is clearly important to determine, with as much precision as possible, what relations exist between the seedling structure, and the size, form, habit and general morphology of the species" ((40), p. 3).

A brief survey of the main ascertained facts of seedling habit and anatomy, and a correlation of these facts with the mature habit of the various species must therefore be made, in order to determine whether the points of discussion mentioned above may be decided on our present knowledge of seedlings and their structure[3].

---

[1] Opinions in favour of the primitiveness of diarchy are given by Hill (*New Phytol.* Report of the Discussion at York, 1906), Hill and de Fraine (76), Lee (101, 102), and Tansley and Thomas (165); and of tetrarchy by Arber (2), Compton (40), Sargant (129, 130), Tansley and Thomas (166), and Thomas (168, 169).

[2] Cf. the views of Compton (40) and Thomas (168, 169), who incline to the belief that the arborescent type is the more primitive in Angiosperms, with those of Sargant (130), who considers that the herbaceous type is more likely to be primitive, on account of its greater plasticity.

[3] It may be well to give here a résumé of the chief features of seedling anatomy in general. According to the extended researches of Dr Miles Thomas ((168, 169, 170, 171); see also (172), where the results of earlier papers are summarised), it appears that the variations in seedling anatomy are not due to difference in basal plan, but to the varying behaviour of a common fundamental unit of vascular structure and its associated strands This fundamental unit is the cotyledonary midrib, which is essentially a "double bundle" or "triad," resolving itself, while still actually in the cotyledon, into two groups of phloem with a single protoxylem strand placed between them; associated with this double bundle there are lateral cotyledonary strands of collateral organisation, and the variations in hypocotyl structure are due, in great measure, to "linkage, fusion or independence" of the components of this cotyledonary vascular system, and to their relative position and state of development (Holden and Clarke (82), p. 335). The stage at which plumular development takes place affects the manner in which the epicotyledonary strands exert their influence upon the cotyledonary vascular system at the cotyledonary node; and this, also, is productive of variations in the hypocotyl structure. For example, in hypogeal types with plumular development relatively advanced at an early stage, the plumule traces may remain independent of the cotyledonary strands (Compton (40), pp. 101, 104; see *Cesalpinia sepiaria*, p. 21, Pl. 3, Figs. 53, 54; also the hypogeal climbing Vicieae, p. 107: Davey (43), p. 576; see *Juglans nigra*, pp. 583, 584, Figs. 6, 7). In other cases, the epicotyledonary strands may sooner or later enter into relations with the lateral cotyledonary strands (Compton (40), p. 104).

It should be noted that difference in number and constitution of the cotyledonary strands may occur in species "which show identical hypocotyl structure, so that the number of cotyledon strands in no sense 'controls' the number of groups in the hypocotyl" (Thomas (172), p. 448); nor does the type of vascular arrangement found in the hypocotyl necessarily determine the number of root poles (Holden and Bexon (80), p. 591; Thomas (169), p. 713, Text-fig. 25; cf. 1 and 2, 3 and 4). But it is from the different *behaviour* of these various vascular strands in the cotyledon and hypocotyl that certain types of root structure result, at varying levels below the cotyledonary node; these types are referable either to the "Cruciform" plan, or to the "Diagonal" plan (Thomas (169), p. 698).

According to present knowledge of seedling structure, the cruciform plan is much the more common. Of this plan, there are two main types: the tetrarch type, with four root poles, two in the cotyledonary plane, and two in the intercotyledonary plane; and the diarch type, where only two—the cotyledonary—poles are present (Thomas (169), p. 713, Text-fig. 25, 1–5; p. 730, Text-fig. 42; p. 731, Text-fig. 43).

The comparatively rare diagonal plan is characterised by the fact that there are root poles lying *between* the cotyledonary and the intercotyledonary planes. The types included under this general plan are: diagonal tetrarchy; hexarchy, with the four diagonal root poles *plus* the two cotyledonary poles; octarchy, with the four diagonal poles *plus* the two cotyledonary and the two intercotyledonary poles; and double-diagonal octarchy, in which the eight root poles occur in pairs in the diagonal planes (Davey (43), p. 578, Fig. 1; Thomas (169), p. 713, Text-fig. 25, 6; and p. 727, Text-fig. 41, 1–2).

In all these cases, there is an even number of root poles; an odd number may, however, result from an asymmetrical behaviour of the vascular strands, as, for example, in *Tilia vulgaris* (Holden and Clarke (82)). In this species, normally, the lateral cotyledonary strands become linked with the central strand or triad, and then separate from it again, so that six strands, three from each cotyledon, occur in the hypocotyl; the triads of the two cotyledons form the two cotyledonary root poles, and the lateral strands fuse in pairs, one from each cotyledon, to form the intercotyledonary poles, cruciform tetrarchy thus resulting in the root. Triarchy may, however, occur in *Tilia vulgaris* when the lateral cotyledonary strands on *one* side of the seedling *remain fused* with the midrib, so that only four strands enter the hypocotyl; the "compound" midrib strands form the two cotyledonary poles, and the two "free" laterals fuse to form a third pole. In the same species, pentarchy may result from asymmetry of a reverse type; the lateral cotyledonary strands, having become free from the midrib, as in normal cases, may *remain free* on *one* side of the seedling, while the other two laterals fuse in the ordinary way, so that five root poles are produced.

Tilia vulgaris thus shows the production of an odd number of root poles in a case where plumular influence does not affect the number of strands in the hypocotyl. In some cases, however, an odd number of root poles may result where plumular traces are continued into hypocotyl and root independently; as, for example, in the hypogeal climbing Vicieae, where two of the root poles are formed by the cotyledonary strands, and a third is plumular in origin (Compton (40), p. 107).

While the vascular system of dicotyledonous seedlings in general is comparatively stereotyped, that of monocotyledonous seedlings shows great variety. It has been shown, however, that the triad or double bundle lying in a median position in each cotyledon of Dicotyledons has its equivalent in the twin strands in the single cotyledon of Monocotyledons, the twin strands having been derived by the disappearance of the central protoxylem of the triad, and the production of metaxylem, collateral with the phloem groups of the triad (see Arber (3), p. 172; Thomas (172)). Further, Miss Sargant (129) has brought forward evidence to indicate that the variations in vascular anatomy of monocotyledonous seedlings may be referable to a tetrarch plan. Variations resulting in polyarchy are due partly to the characteristically broad sheathing

The arrangement of the orders and families reviewed in this section follows Engler's System (49), and reference has been made, where necessary, to the work of Lubbock (107), for seedling habit.

Dicotyledons

Verticillatae.

Miss Davey has found that in four species of *Casuarina*, a genus of specialised woody xerophytes, the seedlings are slender and wiry with a relatively long hypocotyl and epigeal germination; root structure is of the typical cruciform tetrarch plan ((43), pp. 579, 580).

Piperales.

In this order, which contains herbs, shrubs and shrubby climbers, the typically epigeal seedlings appear to be characterised by a uniformly diarch root symmetry (T. G. Hill (66, 67), A. W. Hill (65), Chauveaud (35)).

Salicales.

Of this order of woody plants, two species of *Salix*, *S. Caprea* and *S. repens*, have been examined by Miss Davey ((43), p. 580); both possess very small epigeal seedlings and diarch root symmetry. It should be noted that, while *S. Caprea* is definitely arborescent, *S. repens* is a much smaller, though still woody, type of rather variable habit.

Myricales.

Two species of the shrubby genus *Myrica* were found to possess small and wiry seedlings with epigeal cotyledons. The stele of the hypocotyl near the cotyledonary node shows diarch root structure, while that of the root is of the cruciform tetrarch plan ((43), pp. 580–582).

Juglandales.

The arborescent Juglandaceae comprise both hypogeal and epigeal forms. The four species of *Juglans* so far examined have large seeds and seedlings with a short, thick hypocotyl, early plumular development and considerable uniformity in the structure of the hypocotyl. Cruciform tetrarchy occurs in the root stele. The seeds and seedlings of *Carya* are similar to those of *Juglans* in habit and

base of the single cotyledon, which may introduce minor lateral bundles into the hypocotyledonary system; they may also be caused by the internodal abbreviation of the plumule, and the direct, independent passage of plumular traces into the root.

germination, but are smaller; the root structure of *C. olivaeformis* is octarch, and that of *C. amara* hexarch, both forms thus showing a combination of the diagonal and cruciform plans of symmetry. *Pterocarya rhoifolia* has epigeal cotyledons, a long hypocotyl, fairly robust seedling habit, and cruciform tetrarchy of the root stele; and *Fortunea chinensis*, with its smaller seedlings, shows a similar structure and behaviour in germination ((43), pp. 583–587).

Fagales.

The seedlings of the Betulaceae are typically small, with long slender hypocotyls and epigeal cotyledons. In these slender types, root structure is diarch (*Alnus incana* and *A. glutinosa*, *Betula excelsa* and *B. pumila*); diagonal tetrarch (*Alnus cordifolia*); or cruciform tetrarch (in *Carpinus Betulus* and *C. Ostrya*, which have somewhat larger seedlings than the preceding types). *Corylus avellana* possesses a large seedling with fleshy hypogeal cotyledons and early plumular development; the root stele is of the cruciform tetrarch type.

The members of the Fagaceae have typically very robust seedlings, with large, thick, hypogeal cotyledons, as in *Quercus* and *Castanea*; *Fagus*, however, has seedlings with an erect, comparatively slender hypocotyl and broadly expanded, epigeal cotyledons. In the types of which the seedling structure is known, the species of *Quercus* show hexarch root steles with occasional individual variations (e.g. diagonal tetrarchy in one seedling of *Q. Robur*; double-diagonal octarchy and heptarchy in some specimens of *Q. Ilex*). The large robust seedlings of *Castanea sativa* also are hexarch in their root symmetry; while *Fagus sylvatica* shows, apparently, the very constant development of double-diagonal octarchy in the root ((43), pp. 587–595).

The mature habit of members of the Fagales is exclusively woody; and their seedlings are therefore of considerable interest, since they show great diversity of size and habit, and also a wide range of root structure from diarchy (cruciform plan) to double-diagonal octarchy, while there are in addition cases indicating a transition from one type of symmetry to another ((43), p. 594).

Urticales.

The seedlings of members of this order, so far as examined ((43), p. 595; (35), p. 295), are very uniform in their epigeal habit, and in their diarch root symmetry, though they differ considerably in size; the mature habit of the different types studied is also variable, being arborescent (*Celtis australis* and *C. occidentalis*, of the Ulmaceae; *Morus alba* and *Maclura aurantica*, of the Moraceae); herbaceous (*Urtica dioica* and *U. cannabina*, and *Parietaria officinalis*, of the Urticaceae); and a herbaceous climber (*Humulus Lupulus*, of the Moraceae). It should be especially noted that there is considerable similarity of habit and structure between the seedlings of *Urtica cannabina* and *Morus alba* ((43), p. 595).

Polygonales.

The one family of this order, the Polygonaceae, contains chiefly herbs of varying size; the seedlings also vary in size, and diarchy and tetrarchy are both represented (Thomas (168), p. 85).

Centrospermae.

In this order, composed largely of herbs and undershrubs, the largest seedlings are to be found in the Nyctaginaceae, and it is in these seedlings that a cruciform tetrarch structure occurs in the hypocotyl and, in some cases, also in the root; in other cases, the root stele is diarch, after a tetrarch stage in the hypocotyl. Diarchy characterises the smaller and simpler seedlings of all the other families of the order, so far as they have been investigated[1].

Ranales.

This order includes plants of various habit, from small herbs to trees of considerable size. The seedlings of more than fifty species of the Ranunculaceae have been examined[2], ranging from that of the minute annual herb *Myosurus minimus*, to those of the larger herbs *Delphinium* and *Paeonia*, and the shrubbery climbers of the genus *Clematis*. The seedlings vary in size and in slenderness of habit, but agree generally in the possession of epigeal cotyledons, exceptions including some species of *Paeonia* and *Clematis recta*, where they are fleshy, and do not escape from the seed. Root-like structure is typically found at a high level in the hypocotyl, and the structure of the root itself is uniformly diarch; in two species of *Clematis* a tetrarch stage is temporarily present in the hypocotyl.

Decaisnea Fargesii, a woody type belonging to the Lardizabalaceae, has been found to possess a robust seedling, with a long hypocotyl, epigeal cotyledons, and diarch root structure (Thomas (169), p. 709).

Of the Berberidaceae, the genus *Berberis*, comprising shrubby

---

[1] Hill (68), Hill and de Fraine (74); see also Thomas (169), p. 729, where it is noted that only about 6 per cent. of the Centrospermae show tetrarchy.

[2] Thomas (169), pp. 701–708; see also Chauveaud (35), Gérard (56), Sargant (129), Sterckx (159), Tansley and Thomas (165).

types, shows both diarch and tetrarch root structure; the seedlings vary somewhat in size, but are comparatively slender, with epigeal cotyledons. A point of interest is that the small seedling of *B. Lycium* has a tetrarch root, while the larger seedling of *B. aristata* may show a reduction to triarchy; further, tetrarchy and diarchy both occur in *B. macrophyllum* ((169), pp. 708, 709).

In the Magnoliaceae, a family of shrubby and arborescent forms, the seedlings figured by Dr Thomas are robust with epigeal cotyledons. Three species of *Magnolia* show tetrarchy, and one species diarchy of the root stele. *Liriodendron tulipifera* shows a tetrarch stage in the hypocotyl, while the root itself is diarch ((169), pp. 709, 710).

The species of the Calycanthaceae (shrubs) are characterised generally, so far as they are known, by the possession of diagonal tetrarch root symmetry ((169), p. 711).

Two species of *Anona* (Anonaceae, a family of woody forms) show diarchy of the root stele; and the Lauraceae, also woody, show tetrarchy ((169), pp. 711, 712).

Thus, while the herbaceous Ranunculaceae have uniformly diarch root steles, the more woody families of the Ranales exhibit considerable variation in structure, cruciform tetrarchy being frequent. A very significant feature of the order is the almost invariable presence, at an early stage of epicotyl development, of a cambium connecting the vascular strands; this occurs even in the herbaceous Ranunculaceae, where cambium is absent at a later stage (Blackburn (23), p. 179). In certain cases amongst the Ranunculaceae, cambium has been recorded not only in the epicotyl, but also in the hypocotyl, of young seedlings. In *Eranthis hiemalis*, for example, primary strands of epicotyledonary origin are continued downwards into the hypocotyledonary tuber, where they are connected by a cambium ((23), p. 154); and in *Paeonia herbacea*, the tuberous development of the hypocotyledonary node and the hypocotyl is largely due to rapid growth of the cambium ((23), p. 162); these forms are, however, somewhat specialised, being of geophytic habit.

The very general occurrence of a normal active cambium at the seedling stage of Ranalean types, even where it is absent in the adult plant, suggests the primitiveness of cambial growth and of woody structure for the whole order, an interesting point in view of the fact that, on grounds of floral structure, the Ranales, as a whole, have been considered as basal amongst Angiosperms[1].

---

[1] Arber and Parkin (8, 9); Wernham (185). Cf. however the view of Hutchinson ((87), and (88), pp. 4, 5) that the Ranales (in the generally accepted

Rhoeadales.

This order consists mainly of herbaceous forms, though shrubby types are general in the Capparidaceae; the seedlings vary in size, but are epigeal in their mode of germination. Members of the Cruciferae, Papaveraceae, Resedaceae and Capparidaceae have been examined, and considerable constancy of structure is revealed, diarch root steles characterising the group. It should be noted that two species of *Cleome*, belonging to the typically shrubby family Capparidaceae, show indications of tetrarchy in the hypocotyl ((169), pp. 714–720; (35); (165)).

Rosales.

A large number of members of this order have now been investigated, and considerable variety of seedling root structure has been discovered; there is, of course, a wide range of mature habit exhibited, not only in the order as a whole, but also in individual families, e.g. the Rosaceae and the Leguminosae.

The Crassulaceae, a family of succulent herbs and undershrubs having fleshy seedlings, show diarchy of the root and hypocotyl, so far as known ((169), p. 724).

Of the Saxifragaceae, *Saxifraga muscoides*, *S. Aizoon*, *Heuchera alba* and *Philadelphus grandiflorus* have been examined; their epigeal seedlings are all very slender and have diarch structure in the root and hypocotyl, although there is considerable range in the mature habit of the species, *S. muscoides* being a small alpine herb, and *Philadelphus* a shrub ((169), p. 724).

Those members of the two woody families, Pittosporaceae and Hamamelidaceae, which have been examined showed certain individual peculiarities, making it difficult to decide to which type the root structure should be referred ((169), pp. 725, 726).

The arborescent forms, *Platanus occidentalis* and *P. orientalis* (Platanaceae), have very slender epigeal seedlings with diarch root structure, though a suggestion of tetrarchy is given in the hypocotyl by the presence of four phloem groups ((169), pp. 725, 726).

The members of the Rosaceae show a wide range of structure, diarchy prevailing in the Spiraeoideae and Rosoideae (groups in which the seedlings vary considerably in size, and in which the mature habit is also variable), and cruciform tetrarchy in the woody Prunoideae; while the Pomoideae show diarchy (*Cotoneaster affinis* and *Crataegus*

sense) should be divided into two groups showing parallel floral development: the Ranales (in a restricted sense), representing a primitively herbaceous stock; and the Magnoliales, representing primitively woody types.

Oxyacantha), cruciform tetrarchy (*Pyrus Aria, P. Malus* and *P. communis*), hexarchy (*P. communis*), and heptarchy (one individual of *P. communis*), the two latter types being combinations of the cruciform and diagonal plans of symmetry. The variations in the single species *P. communis* are of interest, for in this case, at least, there is no obvious relation between seedling habit and seedling root structure ((169), pp. 721–724).

Seedling habit and anatomy as correlated with mature habit are very comprehensively known in the Leguminosae, from the work of Professor Compton[1]. The characteristic seedling root structure in the family is cruciform tetrarchy, this being very constant in certain groups, as, for example, in the woody sub-families Mimosoideae and Cesalpinioideae, and in the tribe Phaseoleae (sub-family Papilionatae), which includes herbs, shrubs and trees; in all these tetrarch types the seedlings are characteristically large. The tribe Genisteae, on the other hand, consistently shows diarchy of the seedling root stele, although the seedlings vary greatly in size. The mature habit of members of this tribe is also variable, though on the whole woody; the variation in size of the seedling, however, is not correlated with the variation in size of the mature plant. In the hypogeal Vicieae (Papilionatae), triarchy occurs throughout in connection with rapid plumular development, one of the root poles being plumular. In the Leguminosae as a whole, Compton's work indicates a broad correlation between robust seedlings and cruciform tetrarchy on the one hand, and between the tree habit and the production of large seeds and seedlings on the other; with reduction in the size of the seedlings, there may be traced a corresponding reduction in the number of root poles, resulting ultimately in diarchy.

Geraniales.

Few types of this order have as yet been investigated, the seedling structure of the shrubby genus *Ricinus* (Euphorbiaceae) being the best known (Thomas (170)). The large robust seedling has, typically, a tetrarch root, though variations have been noted in *R. communis* (Chick (36)); and it is stated that the tetrarch type of root symmetry is characteristic for the family (Thomas (168), p. 85).

Sapindales.

Cruciform tetrarch root symmetry, a slender epigeal seedling, and arborescent habit of the mature plant are combined in *Acer*

---

[1] (40); note particularly the tables given on pp. 68–74. See also Holden and Chesters (81); Thomas (169), p. 726; and Gehlen (55).

Pseudoplatanus (Aceraceae) (Holden and Bexon (80); also (168), p. 85). This type is interesting in that it shows a lateral concentration of the vascular strands in the cotyledons, the two phloem and metaxylem groups of the double bundle in each case being detached from the protoxylem and fused with their adjacent lateral strands; four diagonally placed collateral bundles thus enter the hypocotyl, as in *Calycanthus* of the Ranales; but the subsequent behaviour of the bundles leads to cruciform tetrarchy of the root stele in *Acer*, instead of to diagonal tetrarchy as in *Calycanthus* ((80), pp. 591, 592).

Impatiens Roylei (Balsaminaceae), an annual herb, possesses a fairly robust seedling with a long hypocotyl, and tetrarch symmetry of the hypocotyl and root (Holden (78)); the family is said to be characterised by tetrarchy ((168), p. 85).

Malvales.

Of the Tiliaceae, *Tilia vulgaris* has been investigated by Dr Holden and Mr Clarke (82). The seedling is very slender although the mature habit of the species is so markedly arborescent; and the root stele is typically cruciform tetrarch. Plumular development is slow, and the epicotyledonary strands have little effect on the structure of the hypocotyl; triarchy and pentarchy may, however, result from asymmetrical behaviour of the lateral strands of the cotyledonary vascular supply[1].

Althaea rosea (Malvaceae) has been extensively investigated by Miss Bexon (22); this large herbaceous type exhibits considerable variation in root symmetry from tetrarchy to hexarchy, comparable to that shown by the woody type, *Pyrus communis* (cf. Thomas (169), p. 724).

Parietales.

In this order, the seedling structure of the Guttiferae has been examined by M. Brandza (28), who finds that the more slender and normal seedlings of the Hypericoid sub-family—the members of which are typically herbaceous—have diarch symmetry of the root and hypocotyl; the more robust and often tuberous seedlings of the other sub-families, which contain trees and shrubs, are triarch so far as their root steles are concerned, while their hypocotyls show considerable variation in the amount of vascular tissue according to their size.

Opuntiales.

The single family, Cactaceae, is represented by extreme xerophytes with succulent stems and reduced transpiring surface.

---

[1] See footnote, p. 18; cf. triarchy in the Vicieae (Leguminosae).

Pereskia is the least modified type, having large expanded, though fleshy, green leaves; its seedlings, also, are the least modified, while those of the highly specialised Mammillarias are correspondingly modified and tuberous. The seedlings of *Pereskia* and others of the more normal habit (*Opuntia* and *Nopalea*) have tetrarch root steles; while the comparatively small but modified seedlings of *Echinocereus, Echinopsis* and *Mammillaria,* with their swollen hypocotyls and slender roots, show diarchy[1]. The extreme specialisation of the mature habit, and even of the seedling habit, in this family demands caution in considering the results of anatomical studies.

Umbelliflorae.

This order contains both herbs and woody plants, the seedlings being of varying size; they are said to be characterised generally by diarch root symmetry (Thomas (168), p. 85).

Ebenales.

The arborescent and woody plants of this order have fairly large seedlings with a considerable variety of root structure (Thomas (171)). The Sapotaceae are characterised by diagonal tetrarchy ((171); and Smith (156)), which also occurs in species of *Diospyros* (Ebenaceae) ((171); and Wright (197)). Cruciform tetrarchy and diarchy have also been found in the Ebenaceae and Styracaceae.

Tubiflorae.

The seedling structure of a large number of members of this order has been investigated (Lee (101)); and it appears that in the Polemoniaceae, Hydrophyllaceae, Boraginaceae, Labiatae, Solanaceae, Scrophulariaceae and Acanthaceae, characteristically herbaceous families, a diarch root stele is produced; this is the case also in some members of the woody family Bignoniaceae. Tetrarchy occurs in the Convolvulaceae and in *Incarvillea Delayvei* and other members of the Bignoniaceae. In the Tubiflorae, the roots of the smaller seedlings are generally diarch, and those of the larger ones tetrarch, these latter forms comprising about 11 per cent. of the total number investigated ((101), p. 745; Thomas (169), p. 729).

Cucurbitales.

The members of this order are chiefly annual climbing herbs of rapid growth. The seedlings are of various sizes, but are generally large; they are said to be characterised by tetrarchy ((168), p. 85).

---

[1] de Fraine (45); cf. the case of the Guttiferae, where the more normal seedlings have diarch roots, and the swollen types show the larger number of root poles.

Campanulatae.

About fifty species of the Compositae have been examined by Lee (102), who found that, while all the seedlings have diarch or tetrarch roots, so far as known, variations occur in nearly related species, and even in different individuals of the same species. In his diagram, drawn to scale, Lee shows clearly that in this group, at least, there is no close correlation between size of seedling and root anatomy ((102), p. 327, fig. 2; pp. 325, 326).

Monocotyledons

The seedlings of the Monocotyledons show a remarkable variety of structure as contrasted with dicotyledonous seedlings, which are characterised by comparative uniformity of vascular symmetry (Sargant (129); Arber (3), pp. 170 *et seq.*). Although the Monocotyledons are, as a group, typically non-woody, the mature habit varies greatly from that of small herbs (e.g. *Scilla autumnalis*) to that of large fleshy herbs, such as those of the Scitamineae; climbers, such as *Tamus* and *Smilax*, and arborescent forms, like the Palms, Yuccas and *Dracaena*, are also represented. The seedlings, moreover, are very varied in habit and size, though the hypocotyl is generally short, and the primary root and cotyledon are typically short-lived. The vascular structure of the root and hypocotyl may be determined by cotyledonary traces only, as in certain members of the Liliaceae, where plumular development is late; the primary root in such cases tends to be diarch or tetrarch. In cases, on the other hand, where plumular development is early, the structure of the root and hypocotyl is determined by both cotyledonary and plumular traces, and the primary root is often polyarch (see footnote, p. 18). The variation in the stage at which plumular development takes place corresponds to variation in the habit of the species; such development is early in the case of climbers and, more particularly, in that of arborescent species, with their large seedlings and somewhat persistent primary roots; and it is consequently in these cases (e.g. the Palms and *Dracaena*) where the primary root tends to be polyarch; there may be as many as eighteen xylem poles in the root of *Dracaena Draco*.

Gymnosperms

In view of the fact that the Gymnosperms are typically arborescent, or at least woody, in mature habit, mention should be made of their seedling structure by way of comparison with that of the Angiosperms. The seedling habit of the Gymnosperms varies greatly from the robust forms of the Cycads and *Ginkgo* to the slender forms of many of the Coniferae. In the Cycads, the root stele is regarded by Dr Thomas as being typically tetrarch, though many variations occur; for example, in *Cycas siamensis* there is a tetrarch stage in the hypocotyl while the root itself is diarch[1]. *Ginkgo* also shows variation from tetrarchy to diarchy ((168), p. 83; (72)). The seedling roots of the Taxaceae and Pinaceae are typically diarch ((168), p. 84; Hill and de Fraine (70, 71); Chauveaud (34)), though the Araucarians show tetrarchy and even hexarchy in the hypocotyl ((168); (70, 71); Shaw (144)); and many variations occur in connection with polycotyledony in the Abietineae ((70), p. 711; (71), pp. 226, 227). All specimens of the specialised members of the Gnetales which have been examined have diarch seedling roots (Hill and de Fraine (73)). This latter type of root symmetry is, therefore, most common amongst the Gymnosperms (Hill and de Fraine (69)); and it is not entirely correlated with seedling habit for, as Dr Thomas points out, the seedling anatomy of *Ginkgo, Torreya* and *Araucaria* is generally coniferous in type, while the habit is cycadean ((168), p. 84).

The distribution of the various types of seedling root symmetry having been reviewed, and the types correlated as far as possible with seedling habit and mature habit in the different groups, it is necessary to consider whether there is any consistency of association between the arborescent habit and size of seedlings on the one hand, and between size of seedlings and a particular type of root symmetry on the other.

Professor Compton's researches have disclosed, in the Leguminosae, a *general* correlation between the arborescent habit and large seedlings; but there are numerous exceptions to this correlation, some of them even occurring amongst the Leguminosae themselves. In the tribe Genisteae, for example, the seedlings of tree forms such as *Laburnum vulgare* may be slender, and in the Vicieae large seedlings occur in the case of herbaceous species like *Vicia Faba*. Apart from the Leguminosae, notable exceptions to the correlation between the tree habit and large seedlings are to be found in the Betulaceae, where the arborescent types *Alnus* and *Betula* have small and slender seedlings, while those of the less definitely arborescent *Corylus avellana* are large and fleshy. Both large (*Quercus* and *Castanea*) and more slender (*Fagus*) seedlings occur in the arborescent family Fagaceae; and, in other families, *Platanus, Acer* and *Tilia*, all arborescent, have slender seedlings, while those of the herbaceous

---

[1] Thomas (168), p. 82; see also Hill and de Fraine (72), whose table on p. 457 shows considerable variety of root structure.

Cucurbitaceae are comparatively large. A further example of lack of correlation is furnished by the Urticales, the seedling of the herbaceous *Urtica cannabina* being similar in habit to that of the arborescent *Morus alba.*

Amongst the Monocotyledons, it will be seen that large size of the mature plant is to a great extent correlated with large size of the seedlings, as in the Palms and *Dracaena;* but these specialised "arborescent" types cannot validly be compared with the arborescent types of the Dicotyledons, with their normal secondary thickening; large size of seedlings in these Monocotyledons is fairly clearly a physiological necessity, and such specialised cases must therefore be ruled out in phylogenetic considerations.

Finally, a survey of the Gymnosperms, by way of comparison with the Angiosperms, shows a wide variation of seedling size in a typically arborescent group.

The foregoing considerations render it impossible definitely to correlate the arborescent habit with the possession of large seedlings in the Angiosperms, or in fact, in Phanerogams as a whole.

With regard to the second point, Dr Thomas remarks that there is "probably a broad correlation between habit of seedling and root anatomy, but the connexion is by no means close or universal" ((169), p. 731). Professor Compton finds a stable tetrarch root symmetry in large seedlings of the Leguminosae, while the small seedlings tend to show a reduction leading to diarchy ((40), p. 117). Hill and de Fraine contend, as a result of their observations, that the size and structure of seedlings are correlated directly, and remark that tetrarchy appears to be characteristic of large seedlings and diarchy of smaller ones ((76), p. 269). This certainly seems to be the case in the Centrospermae, where the large seedlings of the Nyctaginaceae may have tetrarch roots, while those of other families, generally smaller, have diarch roots. Hill and de Fraine also quote the case of the large seedling of *Dahlia Merckii* with its tetrarch root, comparing it with the smaller seedling of *Coreopsis tinctoria,* where the root is diarch after a tetrarch stage in the hypocotyl ((76), pp. 270, 271).

But, again, there are many exceptions to this correlation of seedling size and structure, some of them being shown by the work of Hill and de Fraine themselves; for example, both the large seedling of *Saponaria Vaccaria* and the small one of *S. cerastoides* have diarch roots (76, 74), and several other pairs of related seedlings differing considerably in size, but showing diarch root symmetry, are noted by these authors (76).

Hill and de Fraine further claim that the seedlings of the Cactaceae show tetrarchy in the case of the large types, and diarchy in that of the small ones ((76), p. 269); but it will be remembered that the "small" seedlings are much modified and have greatly swollen hypocotyls in spite of their slender roots, while the "large" seedlings are the more slender and normal types. In the case of so specialised a family, it is impossible to use the given data in a comparison of this kind; for Hill and de Fraine quote the family in support of their correlation of size and structure, while Dr Thomas refers to its members as showing that there is *not* necessarily a close connection between size and structure ((169), p. 731).

Other cases indicating the impossibility of making a comprehensive statement with regard to the correlation of seedling size and structure may be briefly noted.

Amongst the Juglandales and Fagales, in which, as already shown, the arborescent habit cannot be correlated with seedling size, the large seedlings of *Juglans* possess tetrarch roots while those of the somewhat smaller *Carya* seedlings show hexarchy and octarchy; and the much more slender seedlings of *Fagus* have octarch roots. In these cases, therefore, larger size of seedlings is not correlated with the greater number of root poles (Davey (43), pp. 583–595). In the Ranales, Dr Thomas has shown that tetrarchy of the root stele occurs in the small seedling of *Berberis Lycium*, and that a reduction to triarchy takes place in the larger seedling of *B. aristata*; both the tetrarch and diarch conditions are to be found in different individuals of *B. macrophylla* ((169), pp. 701–714). In the Magnolias also, size and structure cannot be correlated.

A considerable range of variation in the number of root poles occurs in different individuals of *Pyrus communis*, a tree, and *Althaea rosea*, a large herb ((169), pp. 723, 724; Bexon (22)); the variations are similar in type in the two species and, in neither case, have they any relation to the size of the seedlings.

Amongst the Sympetalae, Lee has pointed out the impossibility of definitely correlating seedling size and structure in the Compositae ((102), pp. 325–327).

The Monocotyledons have already been referred to, and rejected as a specialised case, in dealing with the correlation between mature habit and size of seedling; but the polyarchy of large seedlings, for example, those of the Palms, may be noted here. There is clearly a necessity for a large initial vascular supply in the generously proportioned seedling, which gives rise, without secondary growth, to an "arborescent" mature plant; the polyarchy of such Monocotyledons, therefore, cannot be considered as of phylogenetic significance.

While, therefore, in certain restricted circles—for example, amongst the Leguminosae—there may be correlation between size of seedling and a particular type of root symmetry, no general rule can be laid down for the Angiosperms as a whole. As Professor Compton remarks, characters of seedling structure may be of diagnostic value to a limited extent, "but it is exceedingly risky to apply them to solve the broader problems of phylogeny" ((40), p. 118); and though much work on seedling structure has been done since those words were written, it is still not possible to use the given data definitely to decide the primitive habit of Angiosperms; and therefore in this connection it is needless to speculate on the relative primitiveness of tetrarchy or diarchy.

It must be noted, however, that the most cogent piece of seedling evidence concerning the ancestral type of habit for the Angiosperms, is the general occurrence of a cambium at some stage in the seedlings of the Ranales, including those of the herbaceous Ranunculaceae. As already remarked on p. 22, the indications that secondary growth is inherent throughout this possibly basal group are significant as suggesting its derivation, as a whole, from arborescent types.

(2) *The comparative anatomy of the stems of trees, shrubs and herbs*

Professor Jeffrey has concluded, from a study of various types including members of the Ranunculaceae, Nympheaceae and Saxifragaceae, that the primitive vascular condition for the Angiosperms was a solid tubular cylinder, not broken into separate bundles, the cambium being a uniform and continuous layer (90). This view is also held by various other American botanists, who criticise the "Sanio-Sachs-de Bary" description of primary structure and secondary thickening in a dicotyledonous stem which appears so generally in textbooks. This, they contend, implies the development of the woody type, with a continuous cylinder, from the herbaceous type with separate bundles; it further implies, therefore, the primitiveness of the herbaceous habit[1].

---

[1] See Professor Tansley's criticism of this opinion (163). It is pointed out that the older botanists did not necessarily intend to suggest the evolution of woody from herbaceous forms, the phylogenetic standpoint being absent from their writings. On the other hand, the conception of herbaceous types as the origin of woody types seems to have existed in the minds of later botanists, even though it was not definitely expressed; for since the young stages of woody plants are small and herbaceous in texture, it is only logical to conclude, unless anatomical investigations are used as a check, that the herbaceous type came first.

These botanists, notably Jeffrey (90, 91, 92, 93, 94), Bailey (10, 11, 12, 13, 15), Eames (46, 47), Sinnott (145, 150, 154) and Torrey (93, 94), have made extensive anatomical studies to demonstrate their contention that the original woody structure of Angiosperms has become modified to produce the structure characteristic of herbs[1].

While the members of the American school are quite in agreement with regard to this point, they differ amongst themselves as to how the modification of the woody cylinder may have been brought about. There are two rival groups, the supporters of the "foliar ray" (or "aggregate ray") hypothesis, and those of the "decrease of cambial activity" hypothesis.

(*a*) *The "foliar ray" hypothesis.*

As a result of investigations on the origin of the broad rays in the wood of *Quercus* (46) and on the anatomy of the Rosaceae (47), Eames concluded that the original woody cylinder of the angiospermous stem has become modified by the leaf traces and their influence to produce the separate strands of the herbaceous type. The stages in this process may be summarised as follows:

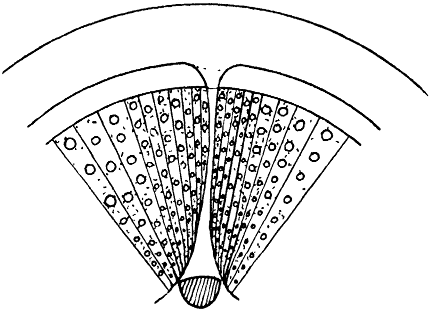

Diagram 2. The aggregation of narrow rays in the neighbourhood of an in-coming leaf trace. (Stippling indicates the presence of fibres.)

(1) The first step in the evolution of the herbaceous type consists in the ordinary narrow rays of the wood of arborescent forms becoming aggregated in the neighbourhood of an in-coming leaf trace (Diagram 2).

---

[1] A further list of researches is given in footnotes 4, p. 1, and 3, p. 2. These studies are concerned in general with wood structures. Hemenway's anatomical studies of the phloem of Dicotyledons are also held to support the theory of the derivation of herbs from woody plants (64); the phylogenetic value of Hemenway's work has, however, been questioned by MacDaniels (108), the range of forms studied not having been sufficiently wide.

(2) The vessels in the bands of wood between these aggregating rays disappear (Diagram 3).

(3) The fibres in the tract opposite and flanking the leaf trace become parenchymatised, so that a "broad ray" or "compound ray" is produced[1] (Diagram 4). Such compound rays are at first shallow, not running vertically for any great distance.

(4) As the herbaceous condition becomes more established, the foliar rays become more homogeneous and vertically elongated; and the flanking parts become increasingly prominent.

(5) The vertical extension of the foliar rays results in the separation of the original continuous woody cylinder into a series of vascular strands arranged in the ring-like manner characteristic of the stems of herbaceous Dicotyledons (Diagram 5). This stage shows the disappearance of the interfascicular cambium and, in many cases, the loss also of the shallow rays within the remaining wood segments (cf. Diagram 6).

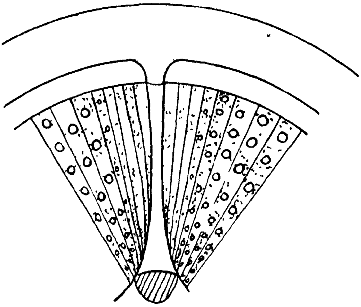

Diagram 3

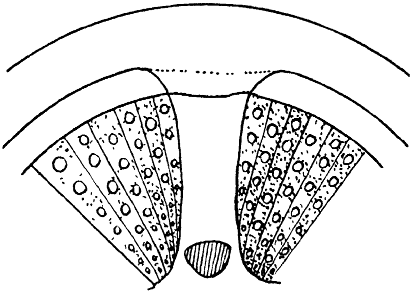

Diagram 4

Diagram 3. The vessels disappear from the bands of wood between the aggregating rays in the neighbourhood of the leaf trace.

Diagram 4. The fibres subtending and flanking the leaf trace become parenchymatised, so that a broad "foliar ray" is produced.

(6) A further modification of the ring of separate strands produces a condition where the cylinder is thinned to such a degree that the *radial* extension of the foliar ray is virtually eliminated.

(7) Finally, by the loss of the fascicular cambium, the "closed

---

[1] It may be noted that this parenchymatisation of wood segments provided an increased food-storage tissue, rendered necessary, very possibly, under certain conditions of climate, namely the unequal seasonal rainfall and temperature of later geological times. See also the suggestion made by Thompson ((177), p. 1011) that in the Mesozoic period leaves probably persisted for several seasons, so that storage devices would be centred about the leaf traces.

bundle" characteristic, for instance, of *Ranunculus repens* (and of Monocotyledons), may be produced (Diagram 7).

Thus, by the development and ultimate loss of the "foliar ray," the herbaceous type of vascular structure may be derived from the woody type (cf. Diagram 8). The chief botanists supporting this view are Jeffrey, Eames, Torrey (90, 91, 92; 46, 47; 93, 94) and, formerly, Bailey (10, 11, 12, 13); with them are associated various younger workers, communications by Adkinson (1), Flint (50), Gates (54), Holden (84, 85), Thompson (177) and Whitaker (186, 187) being especially noteworthy.

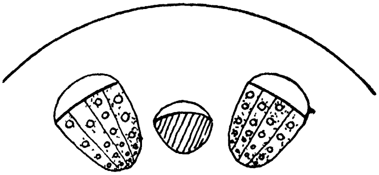

Diagram 5

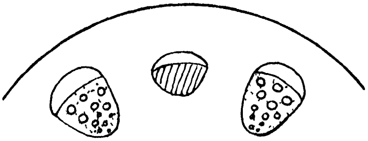

Diagram 6

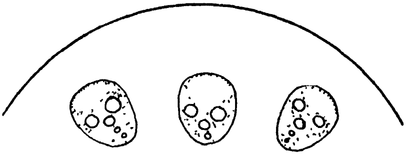

Diagram 7

Diagrams 5, 6, 7. Further stages in the evolution of the herbaceous type of vascular structure (for descriptions, see text). It should be noted that while, according to the "foliar ray" hypothesis, the development of the foliar ray initiates the evolution of the herbaceous type, a decrease of cambial activity accompanies the later stages of its development.

Investigations concerning the process of compounding of ray tissues have included a study of:

(1) The comparative anatomy of normal mature plants, many species of different genera and families being considered.

(2) The life history of individual plants.

(3) Those parts of the plant which are generally considered to retain ancestral characters: namely, the seedling, the reproductive axis and the leaf.

(4) Those parts of the plant which may show a reversion to ancestral characters: namely, the first-formed portion of vigorous mature shoots of plants which have undergone vegetative reduction; and traumatic regions of plants.

(5) Fossil material. This, where available, has been used as a check upon phylogenetic conclusions reached by a study of living plants.

One or two interesting points arising from these researches may be mentioned here.

Bailey, working on numerous members of the Betulaceae and Fagaceae (10, 12, 13), confirmed Eames' conclusions that the broad parenchymatous ray is developed by the aggregation and fusion of uniseriate rays and the parenchymatisation of fibres included between them. The genus *Alnus* demonstrates this point. *A. rhombifolia* and *A. maritima* possess the broad parenchymatous ray in the mature wood, although fusion is apparently not complete in *A. maritima*; in the life history of these two species, stages in the aggregation of rays have been disclosed, the seedling having uniseriate rays. This, according to Bailey, indicates that primitive alders possessed only uniseriate rays, such as occur normally in Coniferae and some other Gymnosperms. A consideration of traumatic reactions has led the same author to conclude that the uniseriate ray is the primitive type in oaks also[1].

An interesting set of facts has been contributed by Miss Adkinson with regard to the Vitaceae, a family in which modifications in ray structure may be correlated with habit (1). *Leea* is a tree-like member

---

[1] Bailey (11); see also (13). Professor Groom (57, 58) has criticised the view that the broad ray (in *Quercus*, for example) has been built up by the compounding of narrow rays. After a consideration of various data, he suggests the possibility that the small rays of *Quercus* may have originated by the disintegration of primitive wide rays, although he does not believe that it is as yet possible to decide whether the broad or the narrow ray is primitive in this genus ((57), p. 1002). Tabor's investigation of the seedling stem of *Fagus sylvatica* (see reference in (57), p. 1000) shows that disintegration and integration take place side by side in the same annual ring; this indicates that the processes are determined by physiological needs, so that it is unwise to place too much reliance upon them in phylogenetic considerations.

In the light of Professor Groom's criticisms, it is interesting to note that in 1911 Bailey quoted a series of species of *Alnus* to illustrate the compounding of ray tissue; *A. acuminata* is given at the base of the series as possessing uniseriate rays ((12), p. 226). In 1912, however, Bailey mentions the same species as an example in which the uniseriate rays are *not* primitive, but have been produced by the breaking-up and diffusion of compound rays ((13), pp. 655, 657); it is impossible to say, therefore, in what order the series given in the previous paper should be read. (See the notes and diagram on p. 37, concerning the diffusion of ray tissue.)

of the family, while most other types are tendril climbers. If the arborescent habit is primitive for the group, *Leea* may be expected to show the most primitive ray structure; and this, according to Miss Adkinson, is the case, for both uniseriate rays and the production of broad rays are seen in the wood. In all examined species of *Vitis*, except *V. californica*, the uniseriate rays have disappeared from the mature normal wood, though they occur in the seedling and in the leaf segments of the first annual ring; they also reappear after an injury. *Ampelopsis* and *Cissus* have progressed still further, for they have more completely lost the uniseriate ray, while the vascular cylinder is in separate strands. It is, of course, debatable whether much significance can be attached to the behaviour of the wood structures in a family composed so largely of plants having a specialised habit.

As a result of considerable criticism, the foliar ray hypothesis has been restated by Jeffrey and Torrey, who advance in its support further evidence drawn from the nodal anatomy of a wide range of "transitional types," or "woody herbs" (94, 181).

Before consideration is given to the rival hypothesis concerning the method of evolution of herbs, another possibility with regard to the behaviour of the foliar ray should be mentioned.

As stated above, this ray having once evolved, the dissection of the woody cylinder may have continued until the herbaceous type of structure resulted (Diagram 8). In other cases, however, the foliar (= "compound" or "broad") ray may have become modified, and the arborescent, or at least the woody, habit retained. For example, Thompson found that in the Ericaceae the compound rays have become broken up into smaller rays, each consisting of several series of cells—the so-called "multiseriate" type ((177); see also footnote 1, p. 35) (Diagram 8). This multiseriate ray, according to Thompson, was perhaps acquired with the advent of deciduous foliage, when storage centres round the leaves were no longer required; it still, however, provides a good storing capacity, together with a better relation between storing, conducting and mechanical tissues. It was already in existence, as Thompson points out, in the Cretaceous Angiosperms studied by Stopes and Fujii (161)[1].

Miss Holden found that in the Eastern North American members of the Salicales the modification of the ray structures has been carried a step further. While multiseriate rays occur in regions supposedly

---

[1] See Sinnott and Bailey's criticism of Thompson's views with regard to the development of the multiseriate ray, noted on pp. 38, 39.

retaining relatively primitive characters, uniseriate rays occur in other parts of the plant (85). Miss Holden also investigated the Sapindales, where multiseriate rays are normal, *Aesculus* alone, of the forms studied, showing reduction to the uniseriate condition in the less conservative regions of the plant (84).

Bailey notes a similar reduction to the uniseriate ray condition in *Castanea, Castanopsis* and *Alnus spp.* amongst the Fagales((13), pp. 655 *et seq.*).

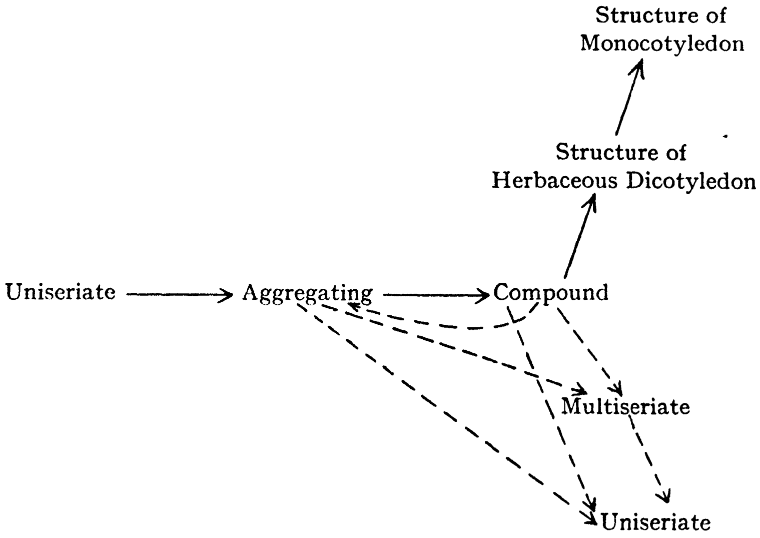

Diagram 8

Therefore, it is claimed, where the woody habit is retained, the foliar or compound ray, having evolved, may be modified and broken up to produce the multiseriate ray; further diffusion of ray tissue may result in the formation of the uniseriate ray (Diagram 8). It is, moreover, possible that any stage or stages may be omitted in the course of evolution; for example, the multiseriate type of ray may arise directly from the "aggregating" type. Also, both aggregate and compound rays may give rise directly to uniseriate rays; and there is further the possibility that aggregate ray stages may be found in the breaking-up of compound rays (Diagram 8).

(*b*) *The hypothesis of "decrease of cambial activity."*

Bailey, once so ardent an exponent of the "foliar ray" hypothesis, has in his later work with Sinnott considerably changed his views (150, 151, 152, 15). While still strongly in favour of the derivation of herbs from woody types, he, with Sinnott, believes that the foliar ray hypothesis is open to objection on various grounds.

In the first place, these authors criticise the great prominence given by Eames to the vascular structure of underground stems in the Rosaceae; they maintain that the use of such stems in determining the factors in the evolution of the herbaceous habit is not legitimate, for in underground organs the absence of mechanical strain and the necessity for storage are liable considerably to modify the structure. Transitions between woody and herbaceous structures should be sought in *aerial* stems, where the actual evolutionary development must have taken place[1].

Secondly, Sinnott and Bailey object to the statement made by Eames, and strongly supported by Jeffrey and Torrey, that the parenchymatised segments of the vascular cylinder have each on their inner border a small primary xylem mass which is a leaf trace, so that the vascular ring consists of alternating large and small bundles. Sinnott and Bailey maintain that in the internode of practically all multifasciculate herbaceous stems, the interfascicular segment of parenchyma has *not* a small leaf trace on its inner margin, and that the stem vascular system is *not* composed of alternating large and small bundles, for the bundles are practically uniform in size[2].

The dissection of the continuous woody cylinder into segments by the development of the foliar ray necessitates the progressive localisation of the primary wood, and such localisation is therefore noted by the advocates of the foliar ray hypothesis as being a distinct feature in the evolution of herbs. Sinnott and Bailey however point out that in certain families composed almost entirely of woody plants, for example, the Araliaceae, Fagaceae, Betulaceae, Proteaceae and others, the ring of primary wood possesses very distinct bundles, while many herbs have a continuous primary ring ((151), p. 555).

In addition to the foregoing general criticisms, Sinnott and Bailey bring forward various other objections to the foliar ray hypothesis, particularly so far as the development of the multiseriate ray is concerned. They point out that multiseriate rays, which are considered by Thompson to be a comparatively recent adaptation to the advent of a severe winter and the consequent acquisition of the

---

[1] Cf. the original statement by Eames ((47), pp. 217–220), and criticism by Sinnott and Bailey ((151), p. 555).

[2] See statement by Eames ((47), pp. 219, 224), criticism by Sinnott and Bailey ((151), p. 555), re-statement by Jeffrey and Torrey (94), and support of their criticism by Sinnott and Bailey (154).

deciduous habit, are yet found in Middle and Upper Cretaceous Dicotyledons. Also, if aggregating and compound rays developed for the purpose of storing food materials descending from the persistent leaves of Mesozoic Angiosperms, and were later replaced by multiseriate rays as an adaptation to cooler conditions, multiseriate rays would hardly be well developed in families which have apparently lived under tropical conditions since ancient times (for example, the Lauraceae, Anonaceae, Ebenaceae and others)[1].

Sinnott and Bailey maintain that in the cases of tropical woody Dicotyledons, of Tertiary and Mesozoic woods, and of types adapted to special habitats (for example, lianes, mangroves, desert plants, semi-herbaceous shrubs, etc.), there is evidence that multiseriate rays of considerable width have originated by the gradual widening of primitive uniseriate rays ((15); (151), p. 558). The widening of narrow rays may also account for the presence of large rays in roots; these certainly cannot be explained by the foliar ray hypothesis.

Taking all these facts into consideration, Sinnott and Bailey have decided that the aggregate or foliar ray hypothesis of the evolution of herbs is unsatisfactory, perhaps the most cogent objections to it being:

(1) That it is based on a study of nodal anatomy and not on that of the whole stem.

(2) That it is complicated and indirect, necessitating the development and ultimate disappearance of the foliar ray, which is the product of aggregation of original parenchymatous rays, and "parenchymatised fibres"—that is to say, it is compounded of distinct structures.

(3) That the woody cylinder of trees is frequently unbroken by foliar rays, while there are a number of herbs which possess a continuous, though narrow, woody cylinder, foliar rays being absent ((154); (15)).

Sinnott and Bailey therefore propose a more simple and direct hypothesis to explain the development of the herbaceous type, their views being supported by the following facts.

In the families Caryophyllaceae, Phytolaccaceae, Hypericaceae, Lythraceae, Onagraceae, Ericaceae and Polemoniaceae, practically all the herbaceous forms are characterised by the possession of an unbroken ring of primary and secondary wood; such a vascular cylinder occurs also in herbaceous genera of many other families. The twigs of woody types related to these herbs show a similar continuous cylinder, wide rays being absent in the secondary wood

[1] See Thompson's original paper on the multiseriate ray (177), and Bailey and Sinnott's criticism of his views (15).

(Diagrams 9, 10). Sinnott and Bailey therefore claim that the herbaceous stem "is essentially the first annual ring of the corresponding woody form, with a reduced amount of secondary growth" ((151), p. 558).

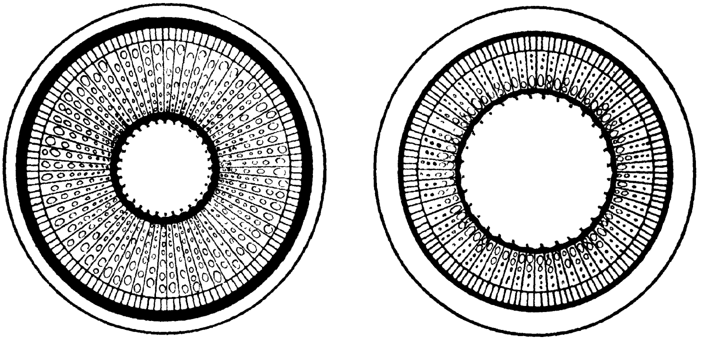

Diagram 9 Diagram 10

Diagrams 9, 10. A woody twig with narrow rays and a continuous protoxylem ring, and a herbaceous stem derived from such a type by simple decrease in cambial activity. (Diagrams from Sinnott and Bailey (151), p. 560.)

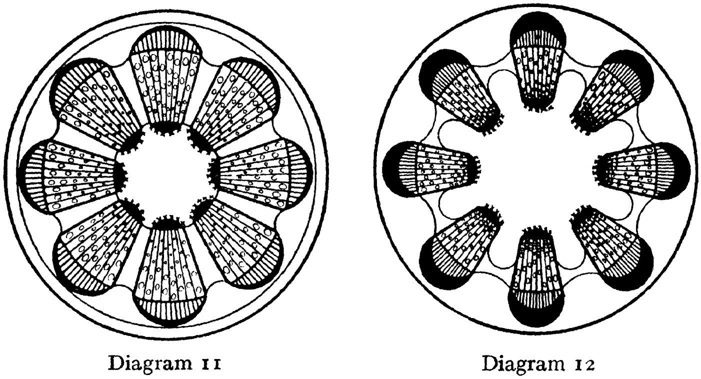

Diagram 11 Diagram 12

Diagrams 11, 12. A woody twig with broad rays breaking the protoxylem ring, and a herbaceous stem derived from such a type by an increase in width of the broad rays, and a decrease in their radial extent. (Diagrams from Sinnott and Bailey (151), p. 557.)

On the other hand, in the case of multifasciculate herbaceous stems of the less reduced type, the interfascicular parenchyma resembles the broad ray of woody plants (Diagrams 11, 12); there is, for example, considerable similarity between the structure of a stout herbaceous stem and that of the first annual ring of *Fagus* ((151), p. 558).

In certain cases, such as *Salvia*, it is recognised that a conversion of segments of the woody ring into fibres or parenchyma has taken place. The process is not, however, comparable with the aggregating and compounding process described by the supporters of the foliar ray hypothesis, for the conversion takes place *between*, and *not opposite*, the protoxylem groups (Diagrams 13, 14) ((151), p. 559).

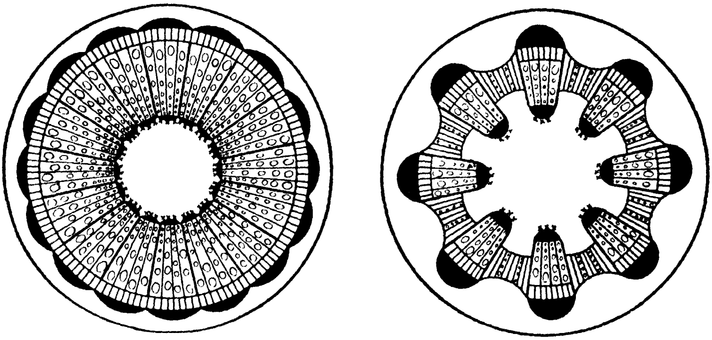

Diagram 13 Diagram 14

Diagrams 13, 14. Woody twig with narrow rays, and a semi-herbaceous stem derived from such a type by partial parenchymatisation of segments *between* the leaf traces; cf. Diagrams 2, 3, 4. (Diagrams from Sinnott and Bailey (151), p. 556. Note that bundles in solid black next the pith represent leaf traces in the stem, and the crosses indicate protoxylem.)

These observations have led Sinnott and Bailey to conclude "that in the development of all herbaceous stems a simple reduction in the amount of secondary wood has been the chief factor"; and this, of course, is due to a decrease of cambial activity. This decrease of cambial activity may be "supplemented by the increase in bulk, to a greater or less degree, of the ordinary parenchymatous tissue"; and this increase of parenchyma, in its turn, may be the result of simple widening of primitive uniseriate rays. Further decrease of cambial activity would, of course, ultimately lead to the monocotyledonous type of vascular structure.

The main point to be emphasised in the anatomical study of the evolution of herbs is that an herbaceous stem in all its essentials is like the first annual ring of its woody relatives. If this has a continuous ring of primary and secondary wood, as do the twigs of woody species of *Nicotiana*, *Hypericum*, and *Hibiscus*..., the corresponding herbaceous stem will show the same features.... If the woody form possesses wider rays and an interrupted primary cylinder, as does *Xanthorrhiza* and the arborescent species of *Acanthopanax* and *Senecio*...its herbaceous representative will show but a slight exaggeration of the same thing.... The whole process of reduction from a woody to an herbaceous condition is therefore a very simple and natural one ((151), pp. 559, 560).

Diagrams 9, 10, and 11, 12, illustrate this hypothesis of the development of the herbaceous type.

It will thus be seen that a study of the comparative anatomy of Angiosperms as outlined above favours the derivation of herbs from woody plants, whether the matter is regarded from the point of view of Jeffrey and his collaborators, or from that of Sinnott and Bailey.

The significance of the inferences from the two hypotheses should be noted. Jeffrey and Torrey point out that if herbaceous Angiosperms have resulted from a decrease of cambial activity, they are *degenerate* ((94), p. 246); and the large development of herbs within the group would therefore indicate that it has passed its zenith and is slowly declining in a manner comparable to that suggested in the case of the Equisetales and Lycopodiales. If, on the other hand, herbaceous Dicotyledons are the result of active advance and differentiation, as Jeffrey and Torrey maintain, they are not degenerate, but *dynamic*, possessing the capacity for further adjustment, modification and evolution.

Mrs Arber's recent work (6) considers the feature—*woodiness*—which, apart from size, especially distinguishes trees from herbs, in a light very different from that of the American botanists, particularly the exponents of decrease of cambial activity.

Mrs Arber asks: "What is the significance of woodiness?" and finds her answer in Church's view that "the transference of plant life from the sea to a subaerial environment, with its intensive insolation, and its relatively inadequate supply of salts, leads to an accumulation of photosynthetic products; the plant under these changed conditions stores sugars, starches and celluloses, because it manufactures them in undue quantities and does not know how to dispose of them" ((6), p. 81). One result of all this accumulation of non-living material is the timber tree (cf. Church (38), pp. 78, 79).

Attention is drawn to the fact that palaeontologists regard the accumulation of non-living material in the animal body as an indication of racial old age; and Mrs Arber suggests that the same may hold good for plants also; so that trees, with their masses of non-living substance, namely woody tissue, are expressive of racial senile degeneration, and must, according to this view, be regarded as a later development within any plant group than the herbs with their much smaller bulk of non-living substance.

Mrs Arber further holds that the frequency of the tree habit in the Angiosperms points

> to the extreme antiquity of the flowering plant stock, which has allowed time for many lineages to reach a phase of senility;.... The tree habit is probably the outcome of a certain fundamental tendency, which is the compensatory drawback to the capacity for photosynthesis—the liability to the accumulation of waste products. It may be hazarded that the earliest symptom of this tendency, historically, was the deposition of a wall round the plant cell;.... The same tendency may be held to have reached an ultimate expression in the massive framework of the forest tree ((6), p. 83).

According to Mrs Arber's view, therefore, it is the *trees*, with their accumulations of non-living, waste material, which are the "degenerate" types amongst the Angiosperms—not the *herbs*, as the hypothesis of decrease of cambial activity would indicate. The herbs represent the earlier habit-form for the group; and it is the frequency of trees, rather than of herbs, which, for Mrs Arber, would indicate that amongst Angiosperms there are at least many forms which have passed their zenith.

Mrs Arber assumes, for the sake of simplicity, that the Angiosperms are monophyletic in origin, so that the primaeval Angiosperm-stock must have been *either* herbaceous *or* arborescent; for her, it is most logical to believe that it was herbaceous. But the group was not necessarily derived from a pro-Angiosperm stock of homogeneous habit; it may have developed along various lines from a stock which *already* contained both herbs and woody forms. So that, while the logic of the claim for *ultimate* primitiveness of herbaceous types is indisputable, neither herbaceousness nor woodiness is necessarily *immediately* and exclusively primitive for the modern Angiosperm group as a whole.

While, *within the group*, herbs may have given rise to woody plants by the accumulation of "waste material," woody plants, on the other hand, may have given rise to herbs, or at any rate herb-like plants, by some process such as that suggested by Sinnott and Bailey in their hypothesis of decrease of cambial activity. As Dr Willis points out, with reference to such genera as *Hypericum*, *Senecio*, and others containing both herbs and woody forms, "It is evident that for nature to form a tree from a herb or shrub, or *vice versa*, is not a specially difficult or unusual feat" ((195), p. 47).

An important point, however, arises out of this statement by Dr Willis.

Mrs Arber asks ((6), p. 74) whether there are "any herbs which in themselves give evidence of a tree ancestry," and in answer to the question draws attention to an investigation made by Dr Burtt Davy (44). This author describes certain sub-shrubs and "herbs" from the High-veld of the Transvaal; and since these plants belong to genera which are represented elsewhere exclusively by woody plants, he regards them as transition types in the evolution of herbs from trees under special environmental conditions. After an examination of evidence concerning three of these plants—*Eugenia pusilla, Erythrina Zeyheri* and *Menodora heterophylla*—Mrs Arber finds that they are essentially woody, though greatly reduced, so much so that their woody development may be almost entirely underground; they are not strictly herbaceous, and cannot, therefore, be accepted as evidence in support of the derivation of herbs from woody plants. On the other hand, Mrs Arber claims that they form an illustration of Dollo's "Law of Irreversibility" (4, 5), according to which "no species in the course of its evolutionary development ever really retraces its steps; it may return to something superficially resembling a stage which it has passed through, but the later is never an exact reincarnation of the earlier stage. On this law we should suppose that if the primaeval Angiospermic stock was herbaceous, a tree lineage arising from this stock might eventually be reduced again to something resembling a herb, but it would not achieve the herbaceous habit with any exactitude; and this seems to be what has happened in the case of these shrublets of the High-veld" ((6), pp. 75, 76).

In view of Mrs Arber's criticism, an anatomical re-examination of stages in the life history, conservative regions, traumatic reactions, etc., would be interesting in the case of those types quoted by Sinnott and Bailey in support of their hypothesis of decrease of cambial activity. It may be that the various series, or at any rate some of them, would reveal increasing, instead of decreasing, woodiness; while other series might show that the "herbs" included in them are really reduced arborescent forms.

(3) *Leaf form, and the vascular supply to the leaf*

Sinnott and Bailey claim that the palmate leaf, probably of lobed outline, represents the primitive type for Angiosperms, and that the pinnate varieties, dominant in recent floras, are derived types (152). Data in support of this view are drawn from conservative regions of the plant, from palaeobotanical evidence, and from phylogenetic considerations, and may be summarised as follows.

(1) Floral leaves (sepals, petals and bracts) are often palmately veined, even in plants where the foliage leaves are pinnately veined, while cotyledons are palmately veined in the majority of Dicotyledons ((152), pp. 8, 9; figs. 25–69). These facts point to palmation as an ancient character persisting in organs generally recognised as conservative.

(2) In present-day floras, varieties of the pinnate type of leaf (particularly simple pinnate) are undoubtedly dominant ((152), p. 3, Table 1), while Sinnott and Bailey claim that from available palaeobotanical evidence, palmate leaves, particularly of lobed outline, appear to have been represented in greater proportion in Cretaceous and Tertiary floras than at the present time ((152), p. 5, Table 2)[1]; this would, of course, indicate that they are the older type.

(3) An examination of the distribution of leaf type amongst the recent members of Angiosperm families shows that the simple pinnate leaf is overwhelmingly predominant in the Metachlamydeae, with their advanced floral morphology; while amongst the Ranales, Rosales and Malvales, considered by some phylogenists to possess the primitive type of floral morphology for the group, palmate leaves, particularly of lobed outline, occur with great frequency ((152), pp. 10–13). In the absence, however, of conclusive evidence as to which group of the Archichlamydeae really presents the most ancient reproductive morphology, this last point must be accepted with caution; for amongst the "Amentiferae," the rival claimants to floral primitiveness, pinnate leaves of various types occur in large proportion[2].

In a separate communication, Sinnott gives an account of the nodal anatomy of a large number of Dicotyledons (145). A foliar supply of three strands, each causing a gap in the stem vascular cylinder, and consequently producing a "trilacunar node," appears to be characteristic of most Dicotyledons, particularly those of the Archichlamydeae ((145), pp. 319, 320) (Diagram 15). Sinnott therefore regards the trilacunar node as being of at least ancient origin in the group, and as constituting a basal type[3]. It is shown that this basal

---

[1] Note that even in these ancient floras, pinnate leaves are the predominant type; cf. the examples figured by Berry (17).

[2] Note that Sinnott and Bailey do not accept the idea of primitiveness of the "Amentiferae" in discussing the primitive type of foliage leaf ((152), p. 11). In connection, however, with their claim for the primitiveness of the "trilacunar node," they mention the group as being amongst the "relatively ancient" Dicotyledons, associating them with the Ranales, Rosales and Malvales ((152), p. 6).

[3] It should be noted that in the Cycadophyta, a unilacunar node appears to represent the primitive state, the dilacunar condition of recent Cycads being a later development (Wieland (189), vol. 1, pp. 66, 67).

type may have been modified both by reduction and by amplification. Reduction by fusion of the three original traces seems to have occurred in the Centrospermae and Tubiflorae; while reduction in the Ebenales, Ericales, Contortae and others has probably taken place by suppression of the two lateral traces. In these cases, a single gap is left in the stem vascular cylinder, and a "unilacunar node" is produced (Diagram 16). Such a node occurs in large proportion amongst the Metachlamydeae ((145), p. 320). A multilacunar node is the result of amplification, that is, of a division of the three original traces; this is found in the Polygonales and Umbelliflorae. Uni-, tri- and multilacunar nodes occur in the Ranales and Rosales, particularly in the families Trochodendraceae, Magnoliaceae and Rosaceae; these are evidently plastic groups so far as nodal anatomy is concerned.

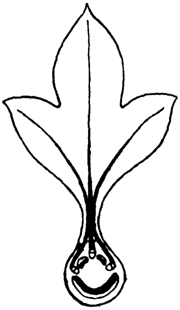

Diagram 15

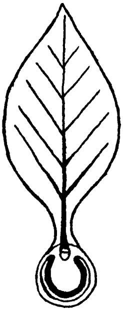

Diagram 16

Diagram 15. A typical modern palmate lobed leaf with cross section of the node (from Sinnott and Bailey (152); see Fig. 84). "The node is trilacunar but the traces are pulled closely together in a narrow petiole before separating again in the lamina."

Diagram 16. A pinnate simple leaf arising from a unilacunar node (from Sinnott and Bailey (152); see Fig. 85); "the single trace continues as a strong midrib."

Sinnott and Bailey find a considerable degree of correspondence between leaf venation and nodal anatomy ((152), p. 7, Table 4)[1]; and they make a reasonable claim for a broad correlation, on the one hand, between the palmate leaf type and the trilacunar node—two characters which they believe to be relatively primitive (Diagram 15); and, on the other hand, between the pinnate leaf type and the unilacunar node—derived characters, the evolution of which may have been determined by the origin of the petiole (Diagram 16) ((152),

[1] See also Sinnott and Bailey's work on the correlation of stipules with the trilacunar node (150).

pp. 13, 14). This "may well owe its development to the fact that the early Angiosperm leaf, ever increasing in breadth of lamina, was in need of a greater flexibility than was afforded by a broad sessile base...." "The primitive leaf with its three traces widely separated in origin passing directly from node to lamina was thus constricted at its base and its three bundles forced close together in the petiole" (cf. Diagrams 15, 17). The petiolar system "seems to have shown an increasing tendency to persist as a single strand," this forming the single midrib of the lamina, and giving off lateral branches in a pinnate manner (Diagram 16).

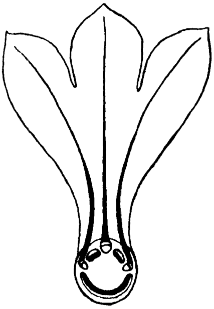

Diagram 17. Reconstruction of the leaf and node claimed by Sinnott and Bailey ((152); see Fig. 83) to be primitive for the Angiosperms. "The node is trilacunar and the veins depart directly into the lamina without approximation in a petiole."

If the suggestions made by Sinnott and Bailey with regard to leaf type and nodal anatomy be admitted, an attempt at further correlation of these characters with habit of growth may yield useful evidence concerning the habit of primitive Angiosperms.

It has already been noted that varieties of the pinnate leaf are strikingly predominant amongst the Angiosperm floras of the present day. They occur, for example, in the arborescent types of the Salicales, Juglandales and Fagales; in shrubby types, such as *Rosa* and *Philadelphus*; and in herbaceous types amongst the Caryophyllaceae, Scrophulariaceae, Campanulatae and Compositae; while they are the general rule amongst the herbs, shrubs and trees of the Leguminosae. The predominance of pinnate leaves thus makes it impossible to correlate them exclusively with any particular habit of growth. It is equally impossible to refer palmate leaves, as a whole, to either woody or herbaceous plants; for they are to be found in *Cercis* and the Maples (trees), in *Ribes* and *Lavatera* (shrubs), and in *Caltha, Delphinium, Saxifraga, Geranium, Malva* and other herbs.

A consistent correspondence between nodal anatomy and habit is also difficult to discover, as will be seen from the following evidence drawn from Sinnott's tabulated summary of nodal type ((145), pp. 319, 320).

While such woody forms as those of the Salicales and Fagales are trilacunar, and such herbaceous forms as those of the Centrospermae and Tubiflorae are unilacunar, numerous discrepancies occur in other groups. For example:

(1) Both herbs and shrubby climbers of the Piperales are tri- and multilacunar.

(2) Herbs, shrubs and trees of the Urticales are as a whole trilacunar.

(3) Amongst the Ranales, the woody Trochodendraceae and Magnoliaceae are uni-, tri- and multilacunar; the herbaceous Ranunculaceae are tri- and multilacunar; while the Anonaceae, Lauraceae and other woody families are unilacunar.

(4) Amongst the Rosales, the herbs, shrubs and trees of both the Rosaceae and Leguminosae are mainly trilacunar; the woody Hamamelidaceae are trilacunar, while the tree forms of the Eucommiaceae are unilacunar.

(5) The woody members of the Sapindales show slightly more unilacunar than trilacunar types.

(6) The Primulales, herbaceous and woody, are all unilacunar; while

(7) The herbs and shrubs of the allied order, Plumbaginales, are trilacunar.

(8) The arborescent Ebenales are unilacunar; and

(9) The typically herbaceous Plantaginales are trilacunar.

(10) The herbs and climbers of the Cucurbitales are trilacunar.

(11) Amongst the Campanulatae, the herbs and woody forms of the Campanulaceae are unilacunar; while the Compositae, a mainly herbaceous family, are mostly trilacunar.

At first sight, therefore, it does not seem possible to establish—between the separate characters of leaf type and nodal anatomy on the one hand, and habit on the other—correlations throwing any light on the primitive growth form of the Angiosperms. The detailed investigations of Sinnott and Bailey, however, reveal the following points:

(1) There is a general association between palmate *simple* leaves and a tri- (or multi-) lacunar node amongst woody plants, though such an association is not so frequent amongst herbs ((152), p. 7).

(2) Practically all the palmate *lobed* and palmate *compound* eaves (as well as a large number of pinnate compound leaves) belong to tri- (or multi-) lacunar species in both woody and herbaceous plants ((152), p. 7).

(3) Amongst woody plants, the trilacunar node predominates only in temperate regions (for example, in the Salicales); in tropical woody plants, the unilacunar node is the more frequent (for example, in the Ebenales) ((152), pp. 15–17).

(4) Amongst woody plants, the palmate lobed leaf is almost entirely confined to temperate regions ((152), pp. 15–17).

The trilacunar node and the palmate lobed leaf appear, therefore, to be linked with the arborescent habit in temperate regions, at least; and this may perhaps be considered as a point in favour of the primitiveness of tree forms in such regions.

The apparent inconsistencies in the correlations of leaf form, nodal anatomy and habit, may be explained by the fact that while various characters may evolve side by side in large groups as a whole, not all the characters evolve together, or at the same rate in different individuals of the group; one character may lag, another proceed rapidly, in different cases, and under different climatic conditions. For example, Sinnott and Bailey suggest that the many species (such as those of the woody Fagales), in which a trilacunar node is associated with the pinnate form of leaf, illustrate "the persistence of an ancient character at the node, which has been lost elsewhere in the leaf" ((152), p. 8). With regard to the effect of climatic conditions, an example may be provided by the development of the unilacunar node in tropical woody plants. This has perhaps been accelerated by the evolution of the large and heavy leaf with its stout, rounded petiole, suited to tropical rain-forest conditions. The point of attachment of such a petiole is circular, instead of elongated as in most woody plants of temperate regions; and this rounded leaf insertion has very probably brought about the concentration of the leaf supply and the development of the unilacunar node ((152), p. 14).

The results of their regional or climatic survey of venation, leaf type and habit, combined with those of their anatomical and other researches on the primitive habit of the Angiosperms, have therefore led Sinnott and Bailey to the conclusion that early Angiosperms were woody plants with trilacunar nodes and palmate leaves, probably of lobed outline (Diagram 17); and that they evolved under temperate upland conditions in early Mesozoic times. Further suggestions made by these writers with regard to the development of the group, are that the main stages of foliar evolution took place while the Dicotyledons were still predominantly woody; that Angiosperms sprang from a palmate coniferous stock, with sessile leaves of the *Araucaria* type, rather than from a pinnate cycadean stock; and, finally, that Monocotyledons, with their parallel venation, were derived from a palmate group of Dicotyledons, very likely at an early stage of Angiosperm evolution, when the palmate leaf was predominant.

(4) *Flower type and habit*

The Ranales, with perfect flowers, and the comprehensive group "Amentiferae," with typically more simply constructed flowers, are rival candidates for the distinction of being considered the most primitive of existing Angiosperms. In either case, the evidence seems to support the hypothesis of the arborescent, or at least woody, nature of primitive Angiosperms[1].

Further, in many instances of orders, families, and even genera containing both woody and herbaceous species, it is possible to distinguish the more primitive—from the floral point of view—from the more highly developed members, and to correlate these floral types with habit. For example, in the Umbelliflorae, the fixed floral plan of the Umbelliferae is correlated with the herbaceous habit, while the more varied, and therefore presumably more primitive, floral structure of the Araliaceae accompanies the woody habit (Sinnott and Bailey (151), p. 563).

In the Leguminosae, 113 of the genera of the two sub-families Cesalpinioideae and Mimosoideae are entirely woody, while the remaining eight genera contain both woody and herbaceous forms. The floral structure of these two groups is generally admitted to be more primitive than that of the Papilionatae which contains a much larger proportion of herbaceous forms ((151), pp. 562, 563). The Compositae, again, with their very advanced floral organisation, consist largely of herbs, there being only 1·5 per cent. of shrubby or arborescent types[2].

The Violaceae provide another example of the broad correspondence between floral structure and habit, for those members of the family which have simple, regular flowers are woody in structure;

---

[1] See references given in footnotes 6 and 7, p. 1; and note especially the seedling evidence suggesting the primitiveness of woodiness for the Ranales as a whole.

[2] Small (155); note that Worsdell (196) interprets the structure of the Compositae as indicating that the herbaceous habit is primitive for the family, a few members of which have become woody; cf. this view with the inferences drawn by Sinnott and Bailey.

the Violeae, with their markedly zygomorphic, and therefore presumably more advanced, flowers, are herbaceous ((151), p. 563).

In the genus *Potentilla*, also, those forms in which the floral structure is considered to be the least advanced are shrubs or undershrubs, while the higher members, from a floral point of view, are all herbaceous ((151), p. 563). Other instances of the same kind occur, amongst individual families or genera, pointing, according to Sinnott and Bailey, to the greater antiquity of the woody type amongst Angiosperms. Mrs Arber ((6), p. 79) adds a further example from the Gramineae, noting that while grasses have usually very reduced flowers, the dendroid Bamboos have flowers which approximate more nearly to the typical monocotyledonous plan; but, as will be shown later, Mrs Arber interprets the correlation of flower type and habit in a different way from Sinnott and Bailey.

Further, if the Dicotyledons are viewed as a whole, 68 per cent. of the genera of the Archichlamydeae are found to be woody, while amongst the Metachlamydeae or Sympetalae, with the more advanced type of floral organisation, more than half the genera are herbaceous. Also, it is an interesting and suggestive fact, according to Sinnott and Bailey, that of the 35 entirely herbaceous families of Dicotyledons, the great majority can have no possible claim to primitiveness, for they are either parasites (Rafflesiaceae), water plants (Callitrichaceae), insectivorous plants (Droseraceae), or they are monotypic (Adoxaceae) ((151), pp. 564, 565).

Sinnott and Bailey therefore conclude that a study of the distribution of herbaceous and woody types in the general system of classification is distinctly in favour of the primitiveness of the arborescent habit amongst Angiosperms.

As already noted, however, Mrs Arber has suggested another interpretation of the correlation of flower type and habit ((6), pp. 77–80). Drawing attention to the shortness of generations in herbs as compared with those in trees, this author notes that "the herb will, in theory, have more numerous chances of exhibiting mutations than the tree. And that this is what has actually taken place, in practice, is shown by statistics of the relative number of species in genera and families of trees and herbs; for it is clear that the existence of a relatively high number of species in a genus or family means that it has been the scene of correspondingly active evolutionary development. Sinnott shows that in the Dicotyledons the average number of species in the woody genera is 12·5, while in the herbaceous genera it is 15. When we reckon by families the difference is more striking, for the woody families average 310, and the herbaceous 510 species to a family. The existence of this *evolutionary lag*—if we may so name it—among trees as compared with herbs is clearly expounded by Sinnott, and yet he hardly seems to appreciate its full significance." According to Mrs Arber, the facts quoted by Sinnott and Bailey in favour of the primitiveness of arborescence, may be explained as due to evolutionary lag, the "necessary outcome of the tree habit." In the case of the Leguminosae for example, especially referred to by Sinnott and Bailey as illustrative of their view, Mrs Arber believes it "more logical to suppose that (they) were originally herbaceous, and that those lineages which adopted the tree habit, put a break, as it were, upon their own evolution, and thus dropped behind the lineages which, by remaining herbaceous, retained the power of mounting the ladder of floral specialisation at a relatively rapid rate."

In connection with a consideration of flower type as correlated with habit, Mrs Arber also draws attention to the work of Ischikawa (89), who, from a general correlation of aberrant embryo sacs with plants of herbaceous habit, argues in favour of the derived nature of such plants. Mrs Arber believes that Ischikawa's evidence is insufficient to allow of its use in this connection; but if it is true that aberrant embryo sacs do occur almost exclusively in plants of herbaceous habit, then her explanation of the more advanced floral structure of herbs may be applied also to cytological details.

(5) *Fruit type and habit*

According to Sinnott and Bailey, Angiosperms with fleshy fruits are very generally of arborescent, shrubby or climbing habit; the dispersal of seed in such cases is usually by the agency of birds, as, for example, in the Rosaceae. Terrestrial herbs, on the other hand, are largely characterised by the possession of dry fruits and seeds, dispersal being effected by explosive and censer mechanisms, or by the agency of the wind, as in *Geranium*, *Papaver*, *Taraxacum*, and many other types (153). Sinnott and Bailey suggest that since frugivorous birds are generally reluctant to feed on the ground[1], the dry fruits of low-growing plants have been developed to meet the needs of seed dispersal. They assume, therefore, a change in fruit type correlated with the change in plant habit from woody to herbaceous. Sinnott further correlates these changes with the

---

[1] Note, however, the damage done to strawberry crops by thrushes and blackbirds.

increase, perhaps even the origin, of ground-feeding birds, such as finches[1].

Fleshy fruits, or rather seeds, seem to have characterised the extinct Gymnosperms, as well as the more primitive living members of the group. They are, therefore, at least of ancient origin; and if their association with primitive Gymnosperms is an index of their own primitiveness, then their occurrence in woody Dicotyledons, such as the Rosaceae, may perhaps signify the primitiveness of the woody habit in Angiosperms. The correlation of fruit type and habit must, however, be made with caution, for dry, wind-dispersed fruits and seeds occur, for example, in *Salix, Populus, Alnus, Betula, Carpinus* and *Ulmus* of the "Amentiferae"; in *Liriodendron* of the Magnoliaceae, and in *Platanus*; also in *Acer, Fraxinus* and the majority of the members of the woody family Bignoniaceae, such as *Catalpa*. Thus dry fruits occur amongst woody Angiosperms which are variously regarded by different writers as primitive, as well as amongst types generally considered to be more advanced. Moreover, many of these genera are of relative antiquity, and their characteristic fruits are known in fossil form, as in the case of *Populus, Betula* and *Acer*; while wind-dispersed winged seeds are associated with the arborescent habit in the Pinaceae amongst Gymnosperms. This frequent occurrence of dry fruits and seeds amongst woody plants indicates that if there has been a change in fruit type, as Sinnott and Bailey suggest, it is a change which has taken place irrespective of habit, and therefore it cannot be said to mark, or to coincide with, the development of herbaceous forms amongst Angiosperms.

Further, it may be pointed out that though fleshy fruits are not very commonly found amongst low-growing plants, they occur, for example, in *Actaea* (Ranunculaceae), in *Fragaria* (Rosaceae) and in *Solanum*; also amongst Monocotyledons, in the Asparagoideae, in *Haemanthus* and certain other Amaryllidaceae, while in *Iris foetidis-*

---

[1] Sinnott (146), p. 297. In this paper, interesting suggestions are made concerning the result of the evolution of herbs. The author is of the opinion that the large development of herbaceous Angiosperms "which has taken place for the most part since the beginning of Tertiary time," has not only had a far-reaching effect upon the aspect of vegetation, but that it has been a determining factor in various lines of development within the animal kingdom, having had, for example, an important relation to the evolution of herbivorous mammals and of ground-feeding birds. Moreover, he suggests that "human society is essentially an herbaceous product," for one of the first steps of primitive man towards civilisation was "to enter the open" and take up agricultural pursuits. The quickly-growing herbs would be the most likely plants to be selected for cultivation; while the practice of animal husbandry is dependent upon herbaceous vegetation ((146), pp. 297, 298).

sima, the seeds possess a fleshy bright-coloured testa. Fleshy fruits and seeds are represented, therefore, in groups considered to be relatively primitive, and also in more advanced types; and it is impossible to say whether or not these latter cases are examples of the retention of a primitive fruit type.

It appears, therefore, that, in the present state of knowledge, a consideration of fruit type contributes little or no evidence of value concerning the primitive habit of Angiosperms.

VI. SUGGESTIONS CONCERNING FUTURE INVESTIGATIONS ON THE PRIMITIVE HABIT FORM OF ANGIOSPERMS

It may be well to conclude this examination of evidence concerning the primitive habit form of Angiosperms by indicating some of the lines along which future investigations on the comparative development of herbs and woody plants may be carried out.

It is only too easy to speak glibly of the effect of changed ecological conditions on the physiological needs of the plant, and to conclude, for example, that the compound ray is a result of the need for increased storage tissue to tide the plant over periods unfavourable to the actual manufacture of food materials; and that the ultimate evolution of the herbaceous habit enables the plant to perennate underground, or in the form of seeds, between growing seasons. It is not intended to imply that these are not legitimate conclusions; but they are apt to be applied to the Angiosperms as a whole, without a real understanding of the structure of the individual plant as determined by its own physiological needs; or without comprehension of the sequence of events which led to the differentiation of its various tissues.

It is necessary, as Professor Tansley has pointed out, to "approach structure through development, the mechanics, physics and chemistry of growth and differentiation"; and to realise that process or function "creates and modifies structure," and is also "in its turn determined by structure." A study of pure morphology alone can never explain structure; a study of process also is necessary[1].

The methods available in a study of "causal morphology" were outlined by Professor Lang in 1915 in his Presidential Address to Section K of the British Association, as follows:

(1) The detailed study in selected plants of the normal development and its results.

---

[1] Tansley (164), pp. 257–259; cf. Bower ((26), p. 169), "the problem of evolution is in its essence physiological." See also Bews (19, 20).

(2) Comparison over as wide an area as possible, with special attention to the essential correspondences arrived at independently.

(3) The study of variation, mutations and abnormalities in the light of their development.

(4) Critical experimental work ((98), p. 704; see also (99)).

A very considerable amount of work has already been done along these lines by Professor Priestley and his collaborators, on the differentiation of endodermis, cork, cuticle and conducting-tissues ((120, 121, 122, 123); see also (124, 125, 126, 127, 128, 157)); by Petersen (115) and by Kostytschew (97) on the differentiation of vascular bundles in the individual; by Professor Thoday on the comparative structure of sunflower stems of different ages and sizes (167); by Professor Holden and his assistants on abnormal seedlings ((78); see also (79, 83, 21)); by Professor McLean Thompson on the developmental morphology of floral structures (109, 110, 111); and by various members of the American school, on physiological and morphological correlations (14, 54, 100, 187, 188, 93).

Work along these lines—and there is still much waiting to be done—will lead to a better understanding of the real causes and determining factors in the development of forms and structures, which, from the purely morphological standpoint, are already familiar.

VII. SUMMARY

The foregoing examination of evidence concerning the primitive habit form for the Angiosperms shows that along certain lines of enquiry the present state of knowledge is so inadequate and inconclusive that no conjecture can reasonably be made from it. This is the case with regard to evidence from the fossil record of the group, and from a consideration of its various fruit types.

Along other lines, the evidence may be suggestive of the primitiveness of either one or the other habit form, though in these cases it is difficult to avoid assumptions and pre-conceived ideas in interpreting the evidence. For example, in a consideration of climatic and geographical distribution of the habit forms amongst the Angiosperms—the results of which are interpreted differently by different writers—there is a tendency, in some cases at least, to assume that plant type and climate were correlated in past ages in the same way in which they are correlated to-day; and this is not necessarily the case.

Taken simply on its own merits, an examination of seedling anatomy is entirely unproductive of decisive evidence concerning the primitive habit of Angiosperms. If, however, the primitiveness of the

Ranalean floral plan is accepted and taken as indicative of the basal position of the order amongst Angiosperms; and if Angiosperms are further assumed to be monophyletic, then the idea of primitiveness of arborescence for the whole group is suggested by the invariable presence of a cambium in the seedlings of the Ranales. Moreover, the same idea having been developed (whether legitimately or not) from such considerations as a comparison of Angiosperms with other plant-phyla, and surveys of their fossil record and of their geographical distribution, it may be held that herbs have developed from trees by, for example, a decrease of cambial activity.

On the other hand, on the single assumption that the Angiosperms are monophyletic, so that the ancestral form must have been *either* herbaceous *or* arborescent, it may very cogently be argued, from various other standpoints, that herbs are primitive and trees derived within the group, the development of tree forms having taken place by the accumulation of non-living woody material. The arguments upon which this view is based are drawn, notably, from enquiries into the significance and cause of the accumulation of woody material, and into the frequent correlation of simple flower type with the tree habit, this latter being explained by the slower maturation of trees, with their consequent longer generations and curtailed opportunities for floral evolution.

It will be realised that the arguments used to determine the primitive habit form of the Angiosperms are, for the most part, highly conjectural; and the fact remains that it cannot as yet be decided, either from direct evidence or from the vast amount of speculative evidence which has been advanced by different writers, what the habit form of the first true Angiosperms really was. Under the circumstances, it is only very tentatively that another suggestion is added to the list: namely, that at some early period, when the predecessors of modern Angiosperms were being differentiated, *both* trees and herbs were represented in the Pro-Angiosperm stock, so that neither type can be considered as *immediately* primitive for the group as a whole. Within the modern group, originally herbaceous stocks may have produced trees, and members of arborescent stocks may have been reduced to herb-like forms. A knowledge of the original habit for circles of relationship can only be further advanced by comprehensive physiological and anatomical studies of the developmental history of individual types; and ultimately, perhaps, such knowledge may indicate what was the composition, with regard to habit, of the ancestral Angiosperm stock.

REFERENCES

(1) Adkinson, J. Some features of the anatomy of the Vitaceae. *Ann. Bot.* **27**, 133. 1913.

(2) Arber, A. The Cactaceae and the study of seedlings. *New Phytol.* **9**, 333. 1910.

(3) —— *Monocotyledons. A Morphological Study.* Cambridge University Press, 1925.

(4) —— The "law of loss" in evolution. *Proc. Linn. Soc.* **131**, 70. 1918–1919.

(5) —— On atavism and the law of irreversibility. *Amer. Journ. Sci.* **48**, 27. 1919.

(6) —— The tree habit in Angiosperms: its origin and meaning *New Phytol.* **27**, 69. 1928.

(7) Arber, E. A. N. *Devonian Floras. A Study of the Origin of Cormophyta.* Cambridge University Press, 1921.

(8) Arber, E. A. N. and Parkin, J. On the origin of Angiosperms. *Journ. Linn. Soc. Bot.* **38**, 29. 1907.

(9) —— —— Studies in the evolution of the Angiosperms: the relationship of the Angiosperms to the Gnetales *Ann. Bot.* **22**, 489. 1908.

(10) Bailey, I. W. Notes on the wood structure of the Betulaceae and Fagaceae. *Forest Quarterly*, **8**, No. 2, 3. 1910.

(11) —— Reversionary characters in traumatic oak woods. *Bot. Gaz.* **50**, 374. 1910.

(12) —— The relation of the leaf-trace to the formation of compound rays in the lower Dicotyledons. *Ann. Bot.* **25**, 225. 1911.

(13) —— The evolutionary history of the foliar ray in the wood of the Dicotyledons, and its phylogenetic significance. *Ann Bot.* **26**, 647. 1912.

(14) —— The significance of the cambium in the study of certain physiological problems. *Journ. Gen. Physiol.* **2**, 519. 1920.

(15) Bailey, I. W. and Sinnott, E. W. Investigations on the phylogeny of the Angiosperms. No. 2. Anatomical evidences of reduction in certain of the Amentiferae. *Bot. Gaz.* **58**, 36. 1914.

(16) Benson, M *Miadesmia membranacea* Bertrand; a new Palaeozoic lycopod with a seed-like structure. *Phil. Trans. Roy. Soc.* B, **199**, 409 1908.

(17) Berry, E. W. *Tree Ancestors. A Glimpse into the Past.* Baltimore, 1923.

(18) —— Supposed Jurassic Angiosperms. *American Naturalist*, **60**, 95. 1926.

(19) Bews, J. W. The ecological evolution of angiospermous woody plants. *Report of the British Association, Oxford*, p. 419. 1926.

(20) —— Studies in the ecological evolution of the Angiosperms. *New Phytologist Reprint*, No. 16. 1927.

(21) Bexon, D. Observations on the anatomy of teratological seedlings. II. On the anatomy of some polycotylous seedlings of *Centranthus ruber*. *Ann. Bot.* **34**, 81. 1920.

(22) —— An anatomical study of the variation in the transition phenomena in the seedling of *Althaea rosea*. *Ann. Bot.* **40**, 369. 1926.

(23) Blackburn, K. On the vascular anatomy of the young epicotyl in some Ranalean forms. *Ann. Bot.* **31**, 151. 1917.

(24) Bower, F. O. *The Origin of a Land Flora.* London, 1908.

(25) —— *The Earliest Known Land Flora.* Lecture at the Royal Institution of Great Britain, April 30, 1920.

(26) —— *Evolution in the Light of Modern Knowledge*, chap. v. Botany. London, 1925.

(27) —— *The Ferns (Filicales)*, **2**. Cambridge, 1926.

(28) Brandza, G. Recherches anatomiques sur la germination des Hypericacées et des Guttifères. *Ann. Sci. Nat. Bot.* sér. 9, **8**, 221. 1909.

(29) Brouwer, J. Dissertation: *Onder-zoekingen over de Platanaceae.* (See also *Rec. Trav. Bot. Néerlandais*, **21**, 369. 1924.)

(30) Bugnon, P. L'origine phylogénétique des plantes vasculaires d'après Lignier, et la nouvelle classe des Psilophytales. *Bull. Soc. Linn. de Normandie*, **7**, 196. 1921 (1922).

(31) Campbell, D. H. *Lectures on the Evolution of Plants.* London, 1899.

(32) —— *An Outline of Plant Geography.* London, 1926.

(33) Carpentier, A. L'origine des Angiosperms et la paléontologie. *Rev. Gén. Sci. Pures et Appl.* **34**, 539. 1923.

(34) Chauveaud, G. Passage de la disposition primitive à la disposition secondaire dans les cotyledons du pin maritime (*Pinus maritima*). *Bull. du Mus. d'Hist. Nat.* No. 7. 1902.

(35) —— L'appareil conducteur des plantes vasculaires. *Ann. Sci. Nat. Bot.* sér. 9, **13**, 113. 1911.

(36) Chick, Edith. On the vascular system of the hypocotyl and embryo of *Ricinus communis* L. *Proc. Roy. Soc. Edin.* **22**, 652. 1900.

(37) Chrysler, M. A. Recent work on evolution in the Dicotyledons. *The Plant World*, **16**, No. 6, 183. 1913.

(38) Church, A. H. Thalassiophyta and the subaerial transmigration. *Botanical Memoirs*, No. 3. Oxford University Press, 1919.

(39) Compton, R. H. Theories of the anatomical transition from root to stem. *New Phytol.* **11**, 13. 1912.

(40) —— An investigation of seedling structure in the Leguminosae. *Journ. Linn. Soc. Bot.* **41**, 1. 1912.

(41) Coulter, J. M., Barnes, C. R. and Cowles, H. C. *A Textbook of Botany.* Vol. II. *Ecology.* New York.

(42) Coulter, J. M. and Chamberlain, C. J. *Morphology of Angiosperms.* New York, 1915.

(43) Davey, A. J. Seedling anatomy of certain Amentiferae. *Ann. Bot.* **30**, 575. 1916.

(44) Davy, J. Burtt. The suffrutescent habit as an adaptation to environment. *Journ. Ecol.* **10**, 211. 1922.

(45) de Fraine, E. The seedling structure of certain Cactaceae. *Ann. Bot.* **24**, 125. 1910.

(46) Eames, A. J. On the origin of the broad ray in *Quercus*. *Bot. Gaz.* **49**, 161. 1910.

(47) —— On the origin of the herbaceous type in Angiosperms. *Ann. Bot.* **25**, 215. 1911.

(48) Eames, A. J. and MacDaniels, L. H. *An Introduction to Plant Anatomy.* New York, 1925.

(49) Engler, A. (with Gilg, E.). *Syllabus der Pflanzenfamilien.* 7th ed. Berlin, 1912.

(50) Flint, E. M. Structure of wood in blueberry and huckleberry. *Bot. Gaz.* **65**, 556. 1918.

(51) Fritsch, F. E. The use of anatomical characters for systematic purposes. *New Phytol.* **2**, 177. 1903.

(52) —— The algal ancestry of the higher plants. *New Phytol.* **15**, 233. 1916.

(53) —— Some aspects of the present-day investigation of Protophyta. *Report of the British Association, Leeds*, p. 176. 1927.

(54) Gates, F. C. A woody stem in *Merremia gemella* induced by high warm water. *Amer. Journ. Bot.* **2**, 86. 1915.

(55) Gehlen, Sister R. Stelar anatomy of *Cicer arietinum* and *Glottidium floridanum*. *Amer. Journ. Bot.* **16**, 781. 1929.

(56) Gérard, R. Recherches sur le passage de la racine à la tige. *Ann. Sci. Nat. Bot.* sér. 6, **11**, 279. 1881.

(57) Groom, P. The evolution of the annual ring and medullary rays of *Quercus*. *Ann. Bot.* **25**, 983. 1911.

(58) —— The medullary rays of Fagaceae. *Ann. Bot.* **26**, 1124. 1912.

(59) Guppy, H. B. Plant distribution from the standpoint of an idealist. *Journ. Linn. Soc. Bot.* **44**, 439. 1919.

(60) GUPPY, H. B. America's contribution to the story of the plant world. *Journ. Ecol.* **9**, 90. 1921.

(61) HALLE, T. G. Einige Krautartige Lycopodiaceen paläozoischen und mesozoischen Alters. *Arkiv f. Bot.* **7**, No. 5, 1. 1908.

(62) —— Lower Devonian plants from Röragen in Norway. *Handl. k. Svenska Vetenskaps-Akad.* **57**, No. 1. 1916.

(63) HALLIER, H. Ein Zweiter Entwurf des Natürlichen (Phylogenetischen) Systems der Blütenpflanzen. *Ber. der deut. bot. Gesellsch.* **23**, 85. 1905.

(64) HEMENWAY, A. F. Studies on the phloem of the Dicotyledons. II. The evolution of the sieve-tube. *Bot. Gaz.* **55**, 236. 1913

(65) HILL, A. W. Morphology and seedling structure of the geophilous species of *Peperomia*, together with some views on the origin of Monocotyledons. *Ann. Bot.* **20**, 395. 1906.

(66) HILL, T. G. The seedling structure of certain Piperaceae. *New Phytol.* **3**, 46. 1904.

(67) —— On the seedling structure of certain Piperales. *Ann. Bot.* **22**, 161. 1906.

(68) —— On the seedling structure of certain Centrospermae. *Report of the British Association, York*, p. 760. 1906.

(69) HILL, T. G. and DE FRAINE, E. On the seedling structure of Gymnosperms. *Ann. Bot.* **20**, 471. 1906.

(70) —— —— On the seedling structure of Gymnosperms. I. *Ann. Bot.* **22**, 689. 1908.

(71) —— —— On the seedling structure of Gymnosperms. II. *Ann. Bot.* **23**, 189. 1909.

(72) —— —— On the seedling structure of Gymnosperms. III. *Ann. Bot.* **23**, 433. 1909.

(73) —— —— On the seedling structure of Gymnosperms. IV. *Ann. Bot.* **24**, 319. 1910.

(74) —— —— On the seedling structure of certain Centrospermae. *Ann. Bot.* **26**, 175. 1912.

(75) —— —— On the influence of the structure of the adult plant upon the seedling. *New Phytol.* **11**, 319. 1912.

(76) —— —— A consideration of the facts relating to the structure of seedlings. *Ann. Bot.* **27**, 257. 1913.

(77) HOAR, C. S. The anatomy and phylogenetic position of the Betulaceae. *Amer. Journ. Bot.* **3**, 415. 1916.

(78) HOLDEN, H. S. Observations on the anatomy of teratological seedlings. III. The anatomy of some atypical seedlings of *Impatiens Roylei*, Walp. *Ann. Bot.* **34**, 321. 1920.

(79) HOLDEN, H. S. and BEXON, D. Observations on the anatomy of teratological seedlings. I. The anatomy of some polycotylous seedlings of *Cheiranthus Cheiri*. *Ann. Bot.* **32**, 513. 1918.

(80) —— —— On the seedling structure of *Acer Pseudoplatanus*. *Ann. Bot.* **37**, 571. 1923.

(81) HOLDEN, H. S. and CHESTERS, A. E. The seedling anatomy of some species of *Lupinus*. *Journ. Linn. Soc. Bot.* **47**, 41. 1925.

(82) HOLDEN, H. S. and CLARKE, S. H. On the seedling structure of *Tilia vulgaris* Heyne. *Journ. Linn. Soc. Bot.* **47**, 329. 1926.

(83) HOLDEN, H. S. and DANIELS, M. E. Observations on the anatomy of teratological seedlings. IV. Further studies on the anatomy of atypical seedlings of *Impatiens Roylei* Walp. *Ann. Bot.* **35**, 461. 1921.

(84) HOLDEN, R. Some features in the anatomy of the Sapindales. *Bot. Gaz.* **53**, 50. 1912.

(85) —— Reduction and reversion in the North American Salicales. *Ann. Bot.* **26**, 165. 1912.

(86) HOSKINS, J. H. A Palaeozoic Angiosperm from an American coal-ball. *Bot. Gaz.* **75**, 390. 1923.

(87) HUTCHINSON, J. Contributions towards a phylogenetic classification of flowering plants. I. *Bull. Misc. Inform Roy. Bot. Gard. Kew*, p. 65. 1923.

(88) —— *The Families of Flowering Plants.* I. *Dicotyledons.* London, 1926.

(89) ISCHIKAWA, M Studies on the embryo sac and fertilisation in *Oenothera. Ann. Bot.* **32**, 279. 1918.

(90) JEFFREY, E. C. The morphology of the central cylinder of the Angiosperms *Trans. of the Canadian Institute*, **6**. 1899.

(91) —— The relations of paleobotany to botany. 2. Morphology. *Amer. Naturalist*, **46**, 225. 1912.

(92) —— *The Anatomy of Woody Plants.* Univ. of Chicago Press, 1922.

(93) JEFFREY, E. C. and TORREY, R. E Physiological and morphological correlations in herbaceous Angiosperms. *Bot. Gaz.* **71**, 1. 1921.

(94) —— —— Transition herbaceous Dicotyledons. *Ann. Bot.* **35**, 227. 1921.

(95) KIDSTON, R. and LANG, W. H On Old Red Sandstone plants showing structure, from the Rhynie Chert-bed, Aberdeenshire. Parts I–V. *Trans. Roy. Soc. Edin.* **51**, **52**. 1917–1921. (Pt. I. *Rhynia Gwynne-Vaughani* Kidston and Lang, **51**, 761. 1917 Pt II. Additional notes on *Rhynia Gwynne-Vaughani* Kidston and Lang; with descriptions of *Rhynia major* n.sp , and *Hornea Lignieri* n.g., n.sp , **52**, 603. 1919–1920. Pt III. *Asteroxylon Mackiei* Kidston and Lang, **52**, 643. 1919–1920. Pt IV. Restorations of the vascular cryptogams and discussion of their bearing on the general morphology of the Pteridophyta and the origin of the organisation of land-plants, **52**, 831 1920–1921 Pt V. The Thallophyta occurring in the peat-bed; the succession of the plants throughout a vertical section of the bed, and the conditions of accumulation and preservation of the deposit, **52**, 855. 1920–1921)

(96) KNOWLTON, F. H. *Plants of the Past.* Princeton University Press, 1927.

(97) KOSTYTSCHEW, S. Der Bau und das Dickenwachstum der Dikotylenstämme. *Ber. der deut bot Gesellsch.* **40**, 297 1922.

(98) LANG, W. H Presidential Address to Section K. *Report of the British Association, Manchester*, p. 701. 1915.

(99) —— The organisation of the plant in the vascular cryptogams in the light of fossil history and causal morphology. *Report of the British Association, Liverpool*, p. 490. 1923

(100) LANGDON, L. M. The ray system of *Quercus alba. Bot. Gaz.* **65**, 313. 1918.

(101) LEE, E. Seedling anatomy of certain Sympetalae. Pt I. Tubiflorae. *Ann. Bot.* **26**, 727. 1912.

(102) —— Seedling anatomy of certain Sympetalae. Pt II. Compositae *Ann. Bot.* **28**, 303. 1914.

(103) LIGNIER, O. Equisétales et Sphénophyllales. Leur origine filicinéenne commune. *Bull. Soc. Linn. Normandie*, sér. 5, **7**, 93. 1903.

(104) —— Sur l'origine des Sphénophyllées. *Bull. Soc. Bot. France*, **55**, 278. 1908.

(105) —— Essai sur l'évolution morphologique du règne végétal. *Compte Rendu Assoc. franç. Av. Sci* 37^{e} session, p. 530. 1908 (1909).

(106) LINDINGER, L. Bemerkungen zur Phylogenie der Monokotylen. *Naturwissen. Wochenschr.* N.F. **9**. 1910.

(107) LUBBOCK, SIR J. *A Contribution to our Knowledge of Seedlings*, **1**, **2**. London, 1892.

(108) MACDANIELS, L. H. The histology of the phloem in certain woody Angiosperms *Amer Journ. Bot* **5**, 347 1918.

(109) MCLEAN THOMPSON, J. The meaning and evolution of some floral characters. *Report of the British Association, Hull*, p. 396. 1922.

(110) McLean Thompson, J. Developmental morphology and its bearing on systematic physiology. *Report of the British Association, Liverpool,* p. 490. 1923.

(111) ——*Studies in advancing sterility*. Publications of the Hartley Botanical Laboratories, Liverpool. Pt I. The Amherstieae. 1924. Pt II. The Cassieae. 1925.

(112) Moss, C. E. Modern systems of classification of the Angiosperms. *New Phytol.* **11**, 206. 1912.

(113) Parkin, J. The *Strobilus* theory of Angiospermous descent. *Proc. Linn. Soc.* March 15th, 1923.

(114) —— Stomata and phylogeny. *Ann. Bot* **38**, 795. 1924.

(115) Petersen, H. E. Some preliminary remarks on the origin of isolated bundles in herbaceous Dicotyledonous plants *Bot. Tidsskr.* **37**, 136. 1920.

(116) Pilger, R. Ueber Verzweigung und Blütenstandbildung bei den Holzgewächsen. *Bibliotheca Bot.* **90**, 1. 1922.

(117) Potonié, H. *Die Metamorphose der Pflanzen im Licht palaeontologischer Thatsachen.* Berlin, 1898.

(118) —— Die Pericaulom-Theorie. *Ber. der deut. bot. Gesellsch.* **20**, 502. 1902.

(119) —— Ein Blick in die Geschichte der Botanischen Morphologie mit besonderer Rücksicht auf die Pericaulom Theorie. *Naturwissen. Wochenschr.* N F. **2**. 1902.

(120) Priestley, J. H. The Endodermis: a study in causal anatomy. *Report of the British Association, Hull,* p. 400. 1922.

(121) —— Physiological studies in plant anatomy. I. Introduction. *New Phytol.* **21**, 58. 1922.

(122) —— Light and growth. II. On the anatomy of etiolated plants *New Phytol.* **25**, 145. 1926.

(123) —— The meristematic tissues of the plant. *Biological Reviews and Biological Proceedings of the Cambridge Phil. Soc.* **3**, 1. 1928.

(124) Priestley, J. H. and Armstead, D Physiological studies in plant anatomy. II. The physiological relation of the surrounding tissue to the xylem and its contents. *New Phytol.* **21**, 62. 1922.

(125) Priestley, J. H. and Ewing, J. Physiological studies, etc. VI. Etiolation. *New Phytol.* **22**, 30. 1923.

(126) Priestley, J. H. and North, E. E. Physiological studies, etc. III. The structure of the endodermis in relation to its function. *New Phytol.* **21**, 113. 1922.

(127) Priestley, J. H. and Tupper-Carey, R. M. Physiological studies, etc. IV. The water relations of the plant growing point. *New Phytol.* **21**, 210. 1922.

(128) Priestley, J. H. and Woffenden, L. M. Physiological studies, etc. V. Causal factors in cork formation. *New Phytol.* **21**, 252 1922.

(129) Sargant, E. A theory of the origin of Monocotyledons founded on the structure of their seedlings. *Ann. Bot.* **17**, 1. 1903.

(130) —— The reconstruction of a race of primitive Angiosperms. *Ann. Bot.* **22**, 121. 1908.

(131) Scott, D. H. *Adaptive Structures in Fossil Plants* Presidential Address to the Linnean Society, 1909.

(132) —— The present position of the theory of descent, in relation to the early history of plants. Presidential Address to Section K. *Report of the British Association, Edinburgh,* p. 170. 1921.

(133) —— *Studies in Fossil Botany.* Parts 1 and 2 London, 1920–1923.

(134) —— *Extinct Plants and Problems of Evolution.* London, 1924.

(135) Senn, G. Die Grundlagen des Hallierschen Angiospermensystem *Beih. z. bot. Cbl.* **27**, 129. 1904.

(136) Seward, A. C. *The Jurassic Flora.* Vol. 2. *The Liassic and Oolitic Floras of England.* Publication of the British Museum, Natural History Department, 1904.

(137) —— *Fossil Plants*, **1–4**. Cambridge University Press, 1898–1919.

(138) —— H. H. W. Pearson, F.R.S., Sc.D. (Cambridge). *Ann. Bot.* **31**, i. 1917.

(139) —— A study in contrasts: the present and past distribution of certain ferns. Hooker Lecture. *Journ. Linn. Soc.* **46**, 219. 1922.

(140) —— A supposed Palaeozoic Angiosperm. *Bot. Gaz.* **76**, 215. 1923.

(141) —— The history of the plant world. *Nature*, **113**, 596. 1924. (Review of Scott (134).)

(142) —— Arctic vegetation past and present. *Journ. Roy. Hort. Soc.* **50**, 1. 1925.

(143) —— Botanical records of the rocks: with special reference to the early *Glossopteris* flora. Presidential Address to Section K. *Report of the British Association, South Africa*, p. 199. 1929.

(144) Shaw, F. J. F. The seedling structure of *Araucaria Bidwillii*. *Ann. Bot.* **23**, 321. 1909.

(145) Sinnott, E. W. Investigations on the phylogeny of the Angiosperms. I. The anatomy of the node as an aid in the classification of the Angiosperms. *Amer. Journ. Bot.* **1**, 303. 1914.

(146) —— The evolution of herbs. *Science* (N.S.), **44**, 291. 1916.

(147) —— Comparative rapidity of evolution in various plant types. *Amer. Nat.* **50**, 466. 1916.

(148) —— Conservatism and variability in the seedling of Dicotyledons. *Amer. Journ. Bot.* **5**, 120. 1918.

(149) —— *Botany: Principles and Problems.* New York, 1923.

(150) Sinnott, E. W. and Bailey, I. W. Investigations on the phylogeny of the Angiosperms. 3. Nodal anatomy and the morphology of stipules. *Amer. Journ. Bot.* **1**, 441. 1914.

(151) —— —— Investigations on the phylogeny of the Angiosperms. 4. The origin and dispersal of herbaceous Angiosperms. *Ann. Bot.* **28**, 547. 1914.

(152) —— —— Investigations on the phylogeny of the Angiosperms. 5. Foliar evidence as to the ancestry and early climatic environment of the Angiosperms. *Amer. Journ. Bot.* **2**, 1. 1915.

(153) —— —— Changes in the fruit type of Angiosperms coincident with the development of the herbaceous habit. *Report of the Bot. Soc. of America*, in *Science*, **41**, 179. 1915.

(154) —— —— The significance of the "foliar ray" in the evolution of herbaceous Angiosperms. *Ann. Bot.* **36**, 523. 1922.

(155) Small, J. The origin and development of the Compositae. *New Phytol.* **16–18**. 1917–1919.

(156) Smith, W. The anatomy of some Sapotaceous seedlings. *Trans. Linn. Soc. Bot.* **7**. 1909.

(157) Soar, I. The structure of the endodermis in some Gymnosperm leaves. *Report of the British Association, Hull*, p. 394. 1922.

(158) Spruce, R. *Notes of a Botanist on the Amazon and Andes*, **1**, **2**. (Edited by A. R. Wallace.) London, 1908.

(159) Sterckx, R. Recherches anatomiques sur l'embryon et les plantules dans la famille des Rénonculacées. *Mém. Soc. Roy. Sci., Liége*, sér. iii, **2**. 1900.

(160) Stopes, M. C. Petrifactions of the earliest European Angiosperms. *Phil. Trans. Roy. Soc.* B, **203**, 75. 1912.

(161) Stopes, M. C. and Fujii, K. Studies on the structure and affinities of Cretaceous plants. *Phil. Trans. Roy. Soc.* B, **201**, 1910.

(162) Tansley, A. G. Reduction in descent. *New Phytol.* **1**, 131. 1902.

(163) —— Notes on recent literature: medullary rays and the evolution of the herbaceous habit. *New Phytol.* **10**, 362. 1911.

(164) Tansley, A. G. Some aspects of the present position of botany. Presidential Address to Section K. *Report of the British Association, Liverpool,* p. 240. 1923.

(165) Tansley, A. G. and Thomas, E. N. Root structure in the central cylinder of the hypocotyl. *New Phytol.* **3**; 104. 1904.

(166) —— —— The phylogenetic value of the vascular structure of spermophytic hypocotyls. *Report of the British Association, York,* p. 761. 1906.

(167) Thoday, D. On the organisation of growth and differentiation in the stem of the sunflower. *Ann. Bot.* **36**, 489. 1922.

(168) Thomas, E. N. A theory of the double leaf-trace founded on seedling-structure. *New Phytol.* **6**, 77. 1907.

(169) —— Seedling anatomy of Ranales, Rhoeadales and Rosales. *Ann. Bot.* **28**, 695. 1914.

(170) Thomas, E. N. Miles. Observations on the seedling anatomy of the genus *Ricinus. Proc. Linn. Soc.* June 21st, 1923.

(171) —— Observations on the seedling anatomy of the Ebenales. *Report of the British Association, Liverpool,* p. 491. 1923.

(172) —— The primary vascular system in Phanerogams, its characters and significance. *Report of the British Association, Toronto,* p. 447. 1924.

(173) Thomas, H. Hamshaw. On a new group of Angiospermous fruits from the Middle Jurassic of Yorkshire. *Report of the British Association, Edinburgh,* p. 452. 1921.

(174) —— The Caytoniales, a new group of Angiospermous plants from the Jurassic rocks of Yorkshire. *Phil. Trans. Roy. Soc.* B, **213**, 299. 1925.

(175) Thomas, H. Hamshaw and Thomas, E. G. On the ancestry of the Caytoniales. *Report of the British Association, Southampton,* p. 364. 1925.

(176) Thomas, H. Hamshaw and others. The relation between the Caytoniales and modern flowering plants. (Discussion at the Linnean Society, Jan. 21st, 1926. See *Proc. Linn. Soc.* p. 22. 1926.)

(177) Thompson, W. P. On the origin of the multiseriate ray of the Dicotyledons. *Ann. Bot.* **25**, 1005. 1911.

(178) —— The anatomy and relationships of the Gnetales. I. The genus *Ephedra. Ann. Bot.* **26**, 1077. 1912.

(179) —— Independent evolution of vessels in Gnetales and Angiosperms. *Bot. Gaz.* **65**, 83. 1918.

(180) —— The relationships of the different types of Angiospermic vessels. *Ann. Bot.* **37**, 183. 1923.

(181) Torrey, R. E. The significance of the "foliar ray." *Science,* **58**, 304. 1923.

(182) Vuillemin, P. L'Amphigonelle et la Phylogénie des Amentales. *Ann. Sci. Nat. Bot.* **10**, 139. 1919.

(183) Walkom, A. B. On *Nummulospermum,* gen. nov., the probable megasporangium of *Glossopteris. Quart. Journ. Geol. Soc.* **77**, 289. 1921.

(184) Wallace, A. R. *Island Life.* London, 1911.

(185) Wernham, H. F. Floral evolution. *New Phytol.* **10**, **11**. 1911, 1912.

(186) Whitaker, E. S. Anatomy of certain golden rods. *Bot. Gaz.* **65**, 250. 1918.

(187) —— Experimental investigation on birch and oak. *Bot. Gaz.* **71**, 220. 1921.

(188) —— Root-hairs and secondary thickening in the Compositae. *Bot. Gaz.* **76**, 39. 1923.

(189) Wieland, G. R. *American Fossil Cycads,* **1**, **2**. Carnegie Institution of Washington, 1906–1916.

(190) —— Classification of the Cycadophyta. *Amer. Journ. of Sci.* **47**, 391. 1919.

(191) WIELAND, G. R. Distribution and relationships of the Cycadeoids. *Amer. Journ. Bot.* **7**, 154. 1920.

(192) —— Progress in palaeobotanical investigations. *Carnegie Institution of Washington, Year Book*, **22**, 353. 1924.

(193) —— Triasso-Jurassic plant evolution and climate. *Amer. Nat.* **59**, 452. 1925.

(194) WILLIS, J. C. The sources and distribution of the New Zealand flora, with a reply to criticism. *Ann. Bot* **32**, 339. 1918.

(195) —— *Age and Area*. Cambridge University Press, 1922.

(196) WORSDELL, W. C. The origin and meaning of medullary (intraxylary) phloem in the stems of Dicotyledons. II. Compositae. *Ann. Bot.* **33**, 421. 1919.

(197) WRIGHT, H. The genus *Diospyros* in Ceylon. *Ann. Roy. Bot. Gard., Peradeniya*, **2**. 1904.

NOTE

Reference should be made to a discussion on "The Antiquity and Early Evolution of the Angiosperms" at the recent International Botanical Congress held at Cambridge, August 16–23, 1930. Dr Hamshaw Thomas re-stated his view that the evolutionary tendencies already detected in the Pteridosperms, Caytoniales and Bennettitales "furnish reasonable grounds for the idea that the Angiosperms were derived from various Pteridosperms early in the Mesozoic period." In reviewing the earlier Mesozoic floras for indications of Angiosperm-like structures, Dr Thomas commented upon the paucity of evidence with regard to stem structure, and referred to Professor R. Kräusel's recent description of *Suevioxylon zonatum*, a wood of Jurassic age from Württemberg, showing dicotyledonous characters (Paläobotanische Notizen, XI. Über ein Jura-Holz vom Angiospermentypus. *Senckenbergiana*, 10, 250, 1928). During the discussion Professor Sahni exhibited a specimen of a fossil wood from the Rajmahal Hills (India); this wood is of great interest, as it is probably of Lower Jurassic age, and is, moreover, similar in structure to that of the Magnoliaceae. It therefore points not only, as does *Suevioxylon*, to the antiquity of the woody habit amongst plants of Angiosperm type but also to the antiquity of the Magnoliaceous type.

It may be noted here that a valuable summary of Dr G. R. Wieland's views regarding the origin of the Angiosperms will be found in the *Proceedings of the International Congress of Plant Sciences (Ithaca)*, 1, 429, 1929.