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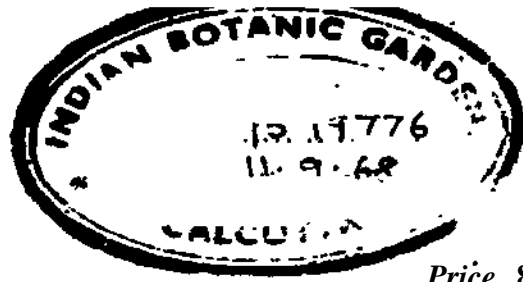
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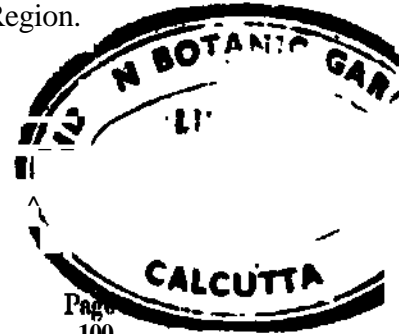
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Biogeographical Relations of **the** New Zealand Region.

By W. R. B. OLIVER, F.L.S., F.Z.S.

(With 7 Text-figures.)

[Read 2nd April, 1925.]



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INTRODUCTION.

THE geographical features which make New Zealand of interest, to **the** plant and animal geographer are the extensive land areas lying in the Pacific Ocean far distant from the nearest continent, the diversity of their physical characters, and the great depth of the surrounding ocean. From a biological view-point the outstanding characteristics of the fauna and flora of the New Zealand region are the absence of mammals, contrasting it with the remainder of the world except Antarctica, the marked dissimilarity of its plant and animal productions to those of Australia, and the presence of an element common to two or more of the southern land masses. No wonder is it, then, that the history of its fauna and flora has often been a matter for discussion among biologists. That New Zealand has been a long time isolated from any other large land mass no one doubts, and that most of its plants and animals are descended from those which reached it over dryland is generally agreed upon by both botanists and zoologists, but in which direction the hind bridge or land bridges lay and at what periods they existed are by no means undisputed points.

In the present paper an attempt is made by an analysis of certain classes of plants and animals of New Zealand to determine the countries between which there has been an interchange of species. The main principle underlying the investigation is one consistent with the theory of descent with modification—namely, that each group has had a single place of origin from which its members have dispersed. The place of origin is not necessarily a small locality, but is coterminous with the area occupied by the parent species of the group in question. The present area of greatest development of a genus is assumed to be the place of origin unless other evidence is available to show that it has shifted. The centre of dispersal of a genus is, therefore, not necessarily supposed to remain always at the place of origin. In the case of a genus endemic in the New Zealand region the relations of the family which includes it are made the basis for determining the point of origin of its antecedents, it being assumed that the ancestors of the genus if traced far enough back would be species having closer relations to those of some other country. For instance, the New Zealand endemic genus *Sporodanthus* may be considered as a descendant of a species which would be included in the same genus as the ancestors of *Lepyrodia* with Australia as the centre of dispersal.

Without being in the least concerned with the place of origin and dispersal of the great phyla of plants and animals, it must be conceded that if New Zealand contains or contained faunas or floras which require continuous land for their dispersal then land connection with some other country is proved. But the demanding of land bridges is not to be held to imply that all the present animals and plants of New Zealand or their ancestors have arrived from some other country. On the contrary, the author believes with Dr. Cockayne («Vegetation of New Zealand/ p. 192, 1921) that many groups have arisen within the New Zealand territory, and further that many species have migrated from it to the surrounding countries.

Before attempting a history of the New Zealand fauna and flora, some general remarks relative to the dispersal of organisms in the Southern Hemisphere will be offered.

#### I. WAYS OF DISPERSAL.

1. Land Bridges.—Most discussions concerning the origin of the fauna and flora of New Zealand, and especially that section of it which has been given the name of Antarctic, have been around the question of former land connections. At one time or another such land bridges have been proposed towards nearly all points of the compass. The easy method by which these hypothetical continents can be brought up from the depths of the ocean has probably been one cause, why the study of geographical distribution has made little advance in recent years; for once a land bridge is assumed, there is no incentive to further investigation. Now, land bridges required on

biological considerations should not conflict with geological evidence—that is, the evidence of the structure of the earth's crust. Geologists, I find, generally rely on paleontological evidence when proposing former land connections. Certain geological evidence, however, will be reviewed because it indicates the direction and time of possible land bridges.

*Contour of Ocean-floor.*—On the principle of the permanence of continental and oceanic areas, past land connections would be indicated by submarine ridges.

The broad features of the contour of the ocean-floor in southern regions consist of submarine platforms less than 2000 fathoms below the surface radiating from the Antarctic continent to New Zealand, the eastern Pacific, South America, the central Atlantic, and the south Indian Ocean. A similar extension, but of greater depth, is indicated towards Tasmania, while South Africa is joined to the central Atlantic ridge. The thousand-fathom line completely surrounds the Antarctic continent, so that any direct land bridge with the north must have been at a remote period.

New Zealand is flanked east and west by deep ocean-trenches. Southwards is the broad submarine ridge just mentioned, while northward is a shallower and more broken extension. Sea-bottom under a thousand fathoms is continuous between New Zealand, Lord Howe Island, and New Caledonia. More broken contours connect New Zealand with the western Pacific by way of Norfolk Island and the Kermadecs respectively. Continental connections, according to the evidence of the ocean-floor, are thus indicated from New Zealand to the north and south, but not to the east or west.

Although in the majority of the series of paleogeographic maps Benson (Trans. N.Z. Inst. vol. liv. 1923) shows a shore-line somewhere near the eastern coast of Australia, he evidently does not consider the Tasman Sea trench a feature of the Paleozoic and Mesozoic periods. But he bases his results largely on the relations of marine faunas, which should be used with caution, as many littoral animals are distributed by means of pelagic larvae or floating objects and depend more on temperature and ocean currents than coast-lines. Kennan has emphasized this point with regard to fishes ('Terra Nova' Report, Zool. vol. i. p. 149, 1916).

The opinion of geologists differ widely regarding the date of origin of the Tasman Sea. Marshall and Morgan think that during the early and mid-Mesozoic era New Zealand was the shore-line of a continent stretching to the westward or north-westward, while Benson draws a map of Australasia in Jurassic times illustrating such a disposition of the land. On the other hand, Arlidge, Schuchert, and Stephens (as quoted by Benson) believed the Tasman Sea to have been early formed, existing in the Jurassic period. It should be pointed out that the existence of the Tasman Sea since the Jurassic period is necessary if the former independent junction of Australia and New Zealand with Antarctic during late Mesozoic times be accepted.

*Periods of Elevation in New Zealand.*—Geological evidence points to the late Palaeozoic as a period when the New Zealand area was elevated, and the land may have extended so as to join other lands. During Palaeozoic times folding, probably pre-Permian, took place along north-west to south-east lines, and at times New Zealand probably formed part of a continent (Morgan, N.Z. Journal Sci. & Tech. vol. v. p. 49, 1922). Recently Park discovered striated boulders in a breccia near Taieri Mouth. He favours a glacial origin, and states that the rocks belong to the Te Anau series, or Upper Carboniferous (Park, Trans. N.Z. Inst. vol. lii. p. 107, 1920).

Glaciation during the Permo-Carboniferous period is known to have been widespread in the Southern Hemisphere. Striated boulders, tillite, or other evidence has been detected in Australia, South Africa, South America, India, and New Zealand. In Australia there are two distinct horizons of glacial origin—one, the Kuttung Series, Carboniferous, and the other, the Bolwurra Conglomerate, Permian (David,<sup>4</sup> 'Guide to Hunter River District,' p. 35, 1923). The glacial phenomena would seem to point to the elevation of the land in various portions of the Southern Hemisphere, and thus connections might be made between Antarctica and one or more of the southern continental lands. Such a radial disposition of the land, instead of the east to west direction that the conception of Gondwanaland implies, might explain the distribution of the glacial phenomena in late Palaeozoic times.

Stephens believed that during Permo-Carboniferous times eastern Australia and New Zealand were independent groups of islands each united with Antarctica (Proc. Linn. Soc. N.S.W. vol. xiv. p. 349, 1889).

The evidence for an extension of land in Permian or early Triassic times is not clear. It rests on the difference between the fossils of the Maitai (Permo-Carboniferous) and Triassic rocks and on the supposed intrusion of plutonic rocks. In New Caledonia middle Triassic rocks are frequently missing.

A continuous series of sediments, mostly unfossiliferous, covers the period from middle Triassic to lower Cretaceous in New Zealand. The direction of the land from which these are derived has not been ascertained, but whether it be east or west, it might fall within the limits of the submarine plateau on which New Zealand stands—that is, the Tasman Sea might have intervened between the land and the Australian terrain.

The Lower Cretaceous period was marked by intense crustal movement in the New Zealand area, resulting in the folding of all the Mesozoic rocks deposited up to that time. According to Morgan, in the south and in the extreme north of New Zealand the folding followed already existing Palaeozoic folding, but elsewhere it commonly took a new direction, north-east to south-west, almost at right angles to the older folding. This was a period of elevation and extension of the land. In New Caledonia no middle Cretaceous rocks are known, so that a long emergence must have been there the feature of that period (Benson, Trans. N.Z. Inst. vol. liv. p. 49, 1923).



Following another period of elevation in Eocene times was a long period of subsidence in the New Zealand area, apparently reaching its lowest limit in the Miocene. Elevation again took place in late Tertiary times, resulting in much block-faulting and tilting.

Summarizing the geological evidence for land connections between New Zealand and other lands, it may be said that elevation is indicated for Permian and perhaps Triassic times, and more certainly in the Lower Cretaceous period. Elevation also took place at the beginning and near the close of the Tertiary epoch. Whether or not land connections with other countries were actually made at any of these periods can best be determined by the biological evidence.

*Marine Faunas.*—I pass over marine faunas as evidence of land connections for the following reasons :—

(1) Marine animals in most cases have free-swimming larvae, many of them being pelagic. In some groups, larvae remain in the swimming stage for a considerable time. Mathews records that the young of *Mytilus edulis* hatched on May 21st, 1912, were swimming on August 15th (Journ. Marine Biol. Assn. vol. ix. p. 557, 1913). The pelagic larvae of littoral molluscs have on several occasions been given distinct generic names, as *Sinusigera*, *Alacgillivrayana*, *Chelotropis*, and so on. Many coastal fishes have in their life-history a pelagic phase, which may be the larval state or the young fish. The marine stages of certain freshwater fishes such as *Galaxias* and *Geotria* come under this head.

(2) Even if marine faunas are held to indicate the presence of a coast-line, continuous land connection does not necessarily follow. There may be one or more straits easily crossed by marine animals, especially if the water be shallow but impassable to land plants and animals.

(3) The community of species in marine fossil faunas indicates like conditions of temperature from which the distribution of ocean currents may be inferred. It would scarcely be safe, however, to map land-lines from this evidence, as currents of different temperatures are sometimes found side by side. The marine fauna in the south of New Zealand is different from that in the north. Here are two ocean currents affecting the coast, but they are not separated by a land barrier. A better-known instance of different faunas on the same coast is that of the eastern United States, where the northern and southern faunas meet at Cape Cod. The marine faunas of the present day are limited usually by temperature in a north and south direction and by land barriers in an east and west direction. With a knowledge only of the limits of the Indo-Pacific region from its fauna no one could possibly map the shore-line. An island area like the Pacific would completely baffle any attempt to do so.

*Palteozoic Floras.*—No plant-remains have so far been detected in rocks of PalaBozoic age in New Zealand. This, of course, does not mean that land did not exist in or near the area. On the contrary, it is evident that there wag

land in the, vicinity of the South Island where fossiliferous rocks of Ordovician, Silurian, and Permian ages occur.

Prior to the late Carboniferous the vegetation of the world was nearly uniform in character. For such a flora, land connections are not indicated in any particular direction. Junctions along lines indicated by present-day ridges would be as good an hypothesis as any other. Similarly, an outward movement from Antarctica along radial land connections before the advancing cold would explain the distribution of the *Glossopteris* flora.

*Mesozoic Floras.*—In several localities in New Zealand floras of Mesozoic age have been described. But up to Jurassic times one type of flora was world-wide in distribution. Land connections in any definite direction, therefore, are not to be inferred from such a flora. That New Zealand was before Triassic time connected with other countries and shared their vegetation is evident enough from the presence of a varied flora of Gymnosperms besides numbers of fern-like plants and Equisetales.

*Present Fauna and Flora as indicating land connections.*—The existing fauna and flora of New Zealand constitute a complex made up of (1) the descendants of species of plants and animals which occupied the New Zealand territory when it was connected with other lands, and (2) species that have arrived overseas or are descended from species that have, arrived overseas. It may safely be said that both these groups contain endemic genera and species—that is, true New Zealand plants and animals that attained their independent rank in the area in which they are now found.

That a connection by continuous land between New Zealand and some other country is necessary to explain the presence of a large proportion of the flora and fauna, is admitted by all. But in what direction the connection or connections lay, at what period in the earth's history they took place, and which plants and animals entered or left New Zealand by such connections are and may always remain matters of contention and conjecture. It is evident, however, that the key to the origin of the present fauna and flora of New Zealand lies in the past changes in the distribution of the land and in the climate, and that the evidence for these must in the first place be biological (including paleontological), but must not conflict with geological evidence. Huxley long ago said that it would hold for the morphologist to give the casting vote on questions of geographic distribution.

2. Ocean Currents.—Granting no connection of the Antarctic continent with land to the north during the Tertiary epoch, except perhaps Graham Land and South America, there would be little alteration in the main currents in the southern ocean to what obtains at present. As the circulation of the atmosphere is in its main features governed by the position of the sun and the rotation of the earth, it may be presumed that the direction of the prevailing winds have not greatly changed. Assuming, then, that the land at its greatest extent was not more than shown in the map herewith (p. 136), there

would be throughout the Tertiary period westerly winds or easterly-moving storms in the south temperate region. The surface currents in accordance with the atmospheric circulation would carry drift in an easterly direction, and an interchange might easily take place between the Antarctic continent and the New Zealand and Australian continents.

The direction of the drift of the surface water of the Southern Ocean at the present day is evidenced by the general northward and eastward movement of icebergs from Antarctic regions. In the South Pacific they reach the latitude of New Zealand. Icebergs have been stranded at the Chatham Islands. In the South Atlantic and Indian Oceans, icebergs pass the 40th parallel of South latitude. Antarctic animals are sometimes stranded on the shores of New Zealand and Australia. The crab-eating seal, for instance, has been recorded twice in New Zealand and twice in Australia. Possibly, however, the northward drift from the Antarctic continent in early Tertiary times when the coast at least supported vegetation may not have been so pronounced as it is now.

The investigations of Grippy ('Plants, Seeds, and Currents in the West Indies and Azores/ p. 310, J 917) show that, from the present direction of currents in the Southern Hemisphere, Australia would receive drift from Fuegia, the islands of the Southern Ocean, and South Africa, and distribute it to the north of New Zealand; while New Zealand would receive drift from Fuegia, the Antarctic continent, the islands of the Southern Ocean, Tasmania, and Southern Australia, and its southern end would distribute it to South Chile.

At present a warm current runs south along the east Australian coast, turning about the latitude of Tasmania towards New Zealand. This current would not come into existence while the Tasman Sea was closed to the north. Instead, the easterly current might be deflected northwards on reaching the New Zealand continent, and coast round the Tasmanian Sea, carrying drift to Australia.

*Drifting Pumice.*—There is an agent of dispersal sufficient to account for the transference of coastal marine forms to all parts of the Pacific, namely drifting pumice. It is cast up on the shores of Australia, New Zealand, and all the islands of Polynesia, and supports corals (Kent, 'Great Barrier Reef,' p. 122, 1893), barnacles, and no doubt many other forms of marine life.

3. Atmospheric Conditions.—The dominant feature of the climate of the south temperate regions is the passage past any given point of a series of easterly-moving cyclonic storms. They take a more southern route in winter than in summer. A second type of cyclonic storms comes to New Zealand from the north-west and affects the northern portion of the Dominion. These are usually summer visitors. The rate of movement of cyclonic storms varies considerably, but averages about 400 miles per day (Pernberton, N.Z. Journ. Sci. & Tech. vol. ii. p. 165, 1919).

The path of cyclonic storms in the late Tertiary period would depend on

the extent of the glaciated area of Antarctica, for these storms coast round the anticyclone area of the polar ice-cap. During the Pleistocene glaciation, therefore, they would be considerably farther north than at present.

**4. Animals.**—Birds as an agent of dispersal need only be referred to here by noting that the Southern Ocean swarms with long-distance flying petrels, which breed in countless numbers among scrub and tussock vegetation on the Subantarctic islands. Probably occasional opportunities are given for the transference of seeds of plants and eggs of animals from island to island by these birds.

## II. MEANS OF DISPERSAL.

All land plants pass through a stage in their life-history specially fitted to endure unfavourable conditions. In spermatophytes it is the seed, in pteridophytes and lower plants the spore. It is during this stage that dispersal most effectively takes place, and the opportunity is given for transportation over long distances. A classification of plants according to whether seed or spore carriage is by wind, water, or animals would be based on inference rather than on observation or experiment; moreover, the seeds or spores of a species might be carried by more than one of these agents. In the following analysis I have given in percentages certain particulars of the floras of Australia and New Zealand and of the non-endemic vascular plants in New Zealand. Figures are first given for those systematic groups which appear specially fitted for wide dispersal—namely, the pteridophytes, orchids, composites, grasses, and sedges. The remainder of the New Zealand plants are then divided according to whether the fruit is fleshy or dry. The results are apparently contradictory, but when other factors, such as the general direction of the movement of plants in the Southern Hemisphere and the age of the groups, are taken into consideration, explanations may be given for these apparent anomalies.

	Australia.	New Zealand.	New Zealand non-endemic.
	10,670 species.	1570 species.	370 species.
Pteridophytes . . . . .	3	10	26
Orchids . . . . .	4	3	4
Composites . . . . .	6	14	5
Grasses . . . . .	4	7	8
Sedges . . . . .	4	8	12
Plants with fleshy fruits. I	79	14	3
Plants with dry fruits not elsewhere included.		44	41

The first three groups are specially adapted for dispersal by wind, yet each gives a different result when the New Zealand non-endemic species are compared with the floras of Australia and New Zealand. The high proportion of pteridophytes is what might be expected in plants with minute

spores capable of being carried long distances by wind. Orchids show no similar high proportion, perhaps because they are a group recently evolved and much specialized. Composites in the New Zealand non-endemic plants show a proportion similar to that of orchids when both are compared with the Australian flora, but when compared with the New Zealand flora they are found to be only about one-third as numerous. They are probably an old group, but they show a greater development in New Zealand than in Australia, and, as will be pointed out later, migration in the south temperate region is mainly from west to east. Hence the proportion of composites found in the New Zealand non-endemic plants, which are mainly also Australian, is low.

The seeds of grasses and sedges may be carried by all agencies, but mainly perhaps by wind and animals. Both, as might be expected, are well represented in the New Zealand non-endemic species. Plants possessing fleshy fruits are usually considered as specially adapted for dispersal by animals. It is significant, therefore, that the proportion of the same in the New Zealand flora, which I consider a continental type, is high, while the percentage in the New Zealand non-endemic plants is quite low.

As most plants are capable occasionally or accidentally of crossing stretches of water, I do not rely greatly on means of dispersal to judge whether they require continuous land connections to explain their present distribution. Rather do I contend that where there has been connection by land the flora which occupied it will, when afterwards divided, show by comparison of the separated parts that they were originally one. The common element will be large and fundamental. There will not be two distinct floras each having but fragments of the other, as appears when the floras of Australia and New Zealand or New Zealand and South America are compared. In one case original continuity of the land is indicated, in the other it is not.

### III. THE MOVEMENT OF SPECIES.

*Life of a Species.*—A point to be considered in connection with the movement of species is the length of life of a species. A species changes in the course of time ; so that whether it gives rise to more than one or not, it eventually changes into what would be considered a distinct species, provided of course it does not become extinct. This statement requires modifying only by saying that some species change more quickly than others. In a change such as this it is evident that isolation is an important condition in originating new species, for those individuals which are free to cross will determine the limits of the changing species. The palaeontological records show that very few species exist as long as the duration of the Tertiary era. From this it follows that if a species is found in lands presumed to have been separated during the whole of the Tertiary period, the probability is that dispersal of that species between the countries in which it is now found is still going on.

The phenomena of swamped genera—that is, those non-endemic but represented in New Zealand by endemic species only—naturally follows from the fact of species changing in course of time, in this case the New Zealand section of the original species running its own course through isolation. Many genera and more species have come into existence as such in the New Zealand region, and the process is still going on.

The age of very few recent species of New Zealand plants can be known, as the paleontological records are scanty. In some cases the relative ages of two groups may be judged by morphological characters, but always with a degree of uncertainty. Willis's 'Age and Area' hypothesis may be useful in suggesting the relative ages of species or the length of time they have been in New Zealand, but independent confirmation is needed.

It should be borne in mind that the disentanglement of the present flora and fauna is complicated by the fact that dispersal has been continuous throughout the ages. Species have arrived and species have departed. There appear, indeed, to be regular migration routes.

*Similar varieties arising in two or more localities.*—Although it is conceivable that a species under similar conditions in two widely-separated countries might in each give rise to varieties which on comparison would appear identical, it is improbable that the new varieties would continue to remain alike for long. The tendency would always be towards differentiation into distinct species. Thus Guppy believes that the variety *Cataracta*? of *Carex Cederi* found in New Zealand, South Africa, and South America is a corresponding varietal modification which has taken place in each region. Likewise I have recorded my opinion that the similarity of the mountain species of *Coriaria* (*C. thymifolia* in the Andes and *C. lurida* in New Zealand) may be due to the fact that each is a derivative of the widespread (*C. ruscifolia*) (Trans. N.Z. List. vol. liii. p. 365, 1921).

*Single point of origin.*—If the plants and animals of New Zealand be examined from the point of view of their probable place of origin and subsequent dispersal, a basis will be established for determining the origin and movements of the flora and fauna. For, assuming the members of a family or generic group to be derived from a common ancestral species, a single point of origin and dispersal follows. The region where the greatest development of a group occurs will usually be where the group originated, but the centre of dispersal may shift. In this case indications of the place of origin may be traced by considering the relationships of the group in question, as in the families *Stylidiaceae* and *Restiaceae* to be mentioned presently.

In very old groups there are probably several whose greatest development is now in the Southern Hemisphere, though they originated in the Northern Hemisphere, where some of them are found fossil in Cretaceous and Tertiary rocks. Some of the Coniferales, as *Agathis*, *Araucaria*, and *Phyllocladus*, also *Fagus* (including *Nothofagus*), appear to come under this category. The principle of the spreading out of successive waves of migration, each a stage

higher than the preceding one, so that old types are found farthest from the centre of dispersal, has been recently pointed out by Matthew (Ann. N.Y. Acad. Sci. vol. xxiv. 1915).

Willis ('Age and Area,' p. 60, 1922) has discovered an important fact in plant-distribution—namely, that if the endemic species of a country be arranged according to the size of their areas of distribution, then more occupy small than large areas. This gives strong support to the principle of a single point of origin for each species. Willis concludes that the older a species the wider its distribution. There can be little doubt, however, that agents for dispersal and opportunity for establishment are the deciding factors in determining the area a species occupies.

In a family, as it extends its area, new points of dispersal arise. Thus the family Stylidiaceae (or Candolleaceae) presumably originated in Australia, where nine-tenths of the species are now found, and spread thence eastward. Reaching New Zealand, a new point of dispersal was formed, resulting in the multiplication of the species of *Forstera*, and the origin of *Oreostylidium* and *Plyllachne*. Even if it be argued that these two genera may have arisen in Australia, travelled to New Zealand, and subsequently became extinct in Australia, it makes only a difference of degree—namely, whether the ancestral species when they crossed the Tasman Sea area were differentiated as genera or not. *Uacline* has reached still farther eastward as far as South America. Equally interesting results are obtained from a study of the family Kestiaceae, which probably originated in South Africa, where most of the genera and species are now found. Some genera like *Retio* and *Hypolena* have species in both countries but fewer in Australia; *Leptocarpus* has more species in Australia than in South Africa, and there are eleven genera of small and medium size confined to Australia. The further extension of the family eastward to New Zealand is precisely of the character of its extension from South Africa to Australia. Of the three species in New Zealand one belongs to an endemic genus, *Sporodanthus* related to a genus, *Lepyrodia*, endemic in Australia; another, *Leptocarpus simplex* is endemic, but belongs to a genus mainly Australian; while the third, *Jypolcena lateriflora*, is identical with an Australian species, and the genus is mainly South African. The distribution of the whole family harmonises with the theory of origin in South Africa, dispersal to Australia by chance crossings during a long period of time, and thence extension to New Zealand in a similar way with long intervals between the arrival of the species.

#### IV. THE MOVEMENT OF FLORAS AND FAUNAS.

*Descent of Faunas and Floras.*—A fauna or flora, like an individual, is the lineal descendant of a previous fauna or flora that in course of time has been modified by inherent changes in the species, and by immigrations and emigrations due to changes in climate or other causes. The study of past floras

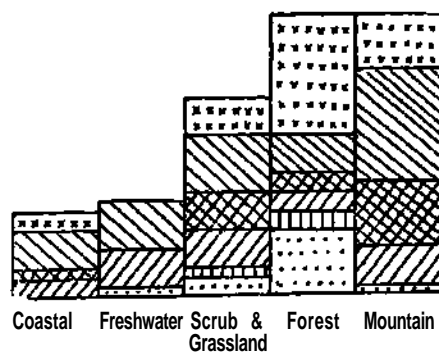
and faunas, especially of the Tertiary period, amply justifies this principle. The Eocene gymnosperms of New Zealand are more closely related to existing species than are those from the Cretaceous. The theory of Ettingshausen that the Tertiary floras of Australia and New Zealand resembled that of Europe more than they resembled the present floras of Australia and New Zealand, has gained wide acceptance notwithstanding the fact that it has either been rejected or ignored by most botanists who have since discussed the relationships of the floras. Ettingshausen's theory rests on the identification of fossil leaves, which shows how the use of characters of small taxonomic value may lead to results inconsistent with the principles of distribution and descent. In point of fact, if Ettingshausen's identifications be accepted, his conclusions would scarcely be justified, as the Tertiary floras of both Australia and New Zealand contain large elements related to the existing floras and not to that of Europe. The reference of European Tertiary species to southern genera like *Eucalyptus* has been discredited and needs revision, as does also the reference of Australian and New Zealand Tertiary plants to northern genera.

*Migration, of Floras.*—In order to make comparisons of different floras with a view to determining those which migrated as a whole and those which have been transferred by occasional means, I have made a comparative analysis of the vascular floras of New Zealand, Lord Howe Island, the Kermadec Islands, and the plants common to New Zealand and Australia and New Zealand and South America (see p. 140). First the plants were divided into five main groups according to habitat—namely, (1) coastal, including all coastal formations subject to the influence of salt air or water; (2) freshwater, comprising swamp, lake, and bog associations; (3) scrub and grassland below the upper limit of forest; (4) forest; and (5) mountain formations, including scrub and grassland above the upper limit of forest. The South Island of New Zealand was taken as the basis for the definition of mountain plants. It was necessary to have some criterion such as this because such mountain plants as reach the islands of the Southern Ocean there descend to sea-level. Each of these five main groups was next divided according to their method and opportunities for dispersal thus: Plants belonging to four groups based on systematic affinity were first counted; these groups are pteridophytes, orchids, grasses, sedges and rushes, and composites. The balance were counted according to whether they were herbs or woody plants. This grouping is admittedly mixed, being based partly on systematic and partly on ecological characters. But from the point of view of dispersal they are comparable, and the features brought out by this classification are, I believe, of some value. Each flora was therefore divided into thirty parts; these were then reduced to percentages and plotted in the accompanying diagrams. The total area is the same in each diagram. For explanation of the diagrams see fig. 6, p. 134.



*The New Zealand Flora* (fig. 1).—New Zealand is an extremely diversified country with a long and varied coast-line, abundance of freshwater streams and lakes; scrub, grassland, and forest extensively developed in both islands; and large areas of mountain country in the South Island, with a smaller area in the North Island. Its flora, therefore, might well serve as a standard for comparison with those of other countries, but my investigations have not led me so far. The percentages of the five main groups utilised in the classification adopted comes very near to multiples of tens, there being two groups each about 10 per cent, of the flora, coastal and freshwater plants; one about 20 per cent., lowland scrub and grassland; and two, each 30 per cent., forest and mountain. The composition of these groups may now be considered. The leading features are these:—There is a small proportion of woody plants in the coastal group, the bulk being herbs, grasses, and sedges. The freshwater plants are about half herbs and about half grasses and sedges. In lowland scrub and grassland

FIG. 1.



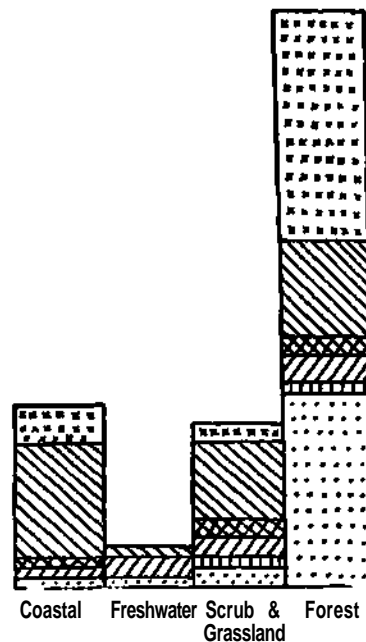
New Zealand Flora (see p. 134).

all groups are fairly well represented. The composition of the forest is important from a distributional standpoint, as the characteristics of forests in continental masses and in oceanic islands differ essentially in features which I have endeavoured to portray. I infer, therefore, that the forest on an island having the same characters as that of a land mass would indicate that it migrated thither by a continuous land connection. The New Zealand forest contains 43 per cent, of woody plants, 23 per cent, of pteridophytes, and the balance about equally divided between the other groups of orchids, grasses, composites, and herbs. The New Zealand mountain plants are strong in woody plants, herbs, and composites.

*Lord Howe Island Flora* (fig. 2).—The flora of Lord Howe Island is introduced for comparison with that of New Zealand because the island has at one time been in direct land connection with New Zealand and New Caledonia, but has been a long time, perhaps for the greater portion of the Tertiary period, isolated and hence subject to oceanic; conditions as regards

dispersal. The flora then should exhibit the characters of a large land area with oceanic elements added, and such, I believe, the analysis here diagrammatically given shows. The island is almost entirely covered with forest, which reaches to the highest point; hence mountain plants are absent. Freshwater conditions are likewise scarcely represented. The percentage of plants in the coastal group is twice as high as in New Zealand. This would follow from the greater length of coast-line in proportion to area in the two places\*. The scrub and grassland group is smaller than in New Zealand, but, like it, contains representatives of all the classes of plants, herbs being especially abundant. The scrub on Lord Howe Island is mainly found on the high cliffs. Forest is naturally the chief feature of the vegetative, covering of

FIG. 2.



Lord Howe Island Flora.

Lord Howe Island. Comparing it with that of New Zealand, it is found to contain 40 per cent. of woody plants and 33 per cent. of pteridophytes, with representatives of all the other groups. In its proportion of woody plants it comes close to the forest of New Zealand, but the percentage of pteridophytes is much higher. Here is evident the influence of oceanic conditions, as the additions to the forest flora since Lord Howe Island formed part of the land bridge to the north of New Zealand would naturally be plants such as ferns, which were able to be transported over oceanic areas. It is also significant in this connection that the proportion of herbs in the Lord Howe Island forest is higher than it is in the New Zealand forest. The forest of Lord Howe Island, then, bears the stamp of having migrated there overland and of having been added to afterwards by occasional means of transport.

Further evidence of the former connection of Lord Howe Island with New Zealand and New Caledonia is furnished by the presence of a flightless rail, *Tricholimnas sylvestris*, and several species of large land shells, including *Placostylus hivaricosus* (see Oliver, Trans. List. N.Z. List. vol. xlix. p. III, 1917;).

*Two Floras in JSew Zealand.*—The analysis so far given does not disclose the presence of different floras in the same area. In New Zealand, for instance, there appear to be intermingled two floras, one in which podocarps, pines, and trees of Malayan affinities are dominant, and another in which *Notkofagus* is the prevalent tree. But the plants associated with *Notkofagus* are likewise mainly plants of Malayan alliances, so that the distinctness of the two types of forest is probably due to age. One is the result of an earlier period of prevalence in New Zealand than the other, the *JS<sup>T</sup>othofagus* forest being the earlier. It has for the most part been displaced by the mixed forest. Both forests are similar in the characters brought out in the diagram, so that both are of continental type. Were the *Nothofugns* forest to be the portion of a forest invading New Zealand from the south, it should be accompanied by a flora of southern facies, South American for instance, and one would expect it to be best represented in the islands to the south of New Zealand. Such, however, is not the case. The forest of the Auckland Islands does not even include *Nothofagvs* as one of its members. Its dominant tree is the southern rata, *Aletrosuferos lucida*, a tree belonging to a genus of Malayan origin.

*Disharmonic Floras.*—If a flora of the constitution of that of New Zealand be termed harmonic, then one departing from it in the character and proportion of all its main groups, but especially of its forest, may be called disharmonic. This term I have borrowed from the writings of zoogeographers, for the floras which cross stretches of ocean by occasional means of transport obey different laws to those which migrate overland. They are the result of an accumulation of species which have accidentally come together; hence they would be expected to lack some of the essential characters of harmonic floras and have others enhanced. Such a disharmonic flora is that of an oceanic island—that is, one that has received its entire flora overseas. Coastal and freshwater floras exhibit no such differences as those found between continental and oceanic forests, but scrub and grassland differ to a small extent in continental and island areas. Before analysing a typical island of the oceanic class, some general remarks on the migration of plants in the southern temperate region will be made.

*Plant-formations and wide dispersal.*—Widely-distributed species of plants are in nearly all cases those belonging to plant-formations which are more or less open and exposed. Forest plants usually are not widely distributed. The reasons for this probably are that the opportunities for having their seeds removed by wind or birds, or, in the case of coastal formations, by ocean

currents, are best afforded in low, exposed formations. The opportunities for establishment are likewise more frequent in open formations than in closed ones. Hence coastal, swamp, scrub, and mountain plants make up the bulk of the widely-ranging species common to two or more of the southern land masses.

The wide distribution of freshwater plants has often been commented on. They form 10 per cent, of the flora of New Zealand, 25 per cent, of the 320 species common to Australia and New Zealand, and 35 per cent, of the 80 cosmopolitan species in New Zealand. Thus the wider ranging the group the higher the percentage of freshwater plants.

Certain portions of White Island off the north-east coast of New Zealand are each summer occupied by gannets, which destroy the vegetation where they breed. When they leave the island a rank growth of herbs springs up in their place. The seeds of these have without doubt been carried, probably by wind and birds, from the mainland, but the birds have made the opportunity for their establishment.

*Distribution in Temperature Zones.*—On comparing the distribution in their respective countries of plants and animals common to Australia and New Zealand, some are found to be restricted to belts bounded by isothermal lines. For instance, a few marine molluscs of southern distribution in Australia are found in the same latitudes in New Zealand. *Mytilus planvatus* and *Argobuccituum tumidum* are examples. Similarly *Tonna cereisina*, *Ostrea cucullata*, and *Mitra carbonaria* occur in the north of New Zealand and in corresponding latitudes in Australia. Plants found in Tasmania but not in Australia and with a southern distribution in New Zealand are *Gaultheria depressa*, *Donatia Novw-Zealandi*, *Utricularia monanthos*, *Liparophyllum Gunnii* and *Ilierochloe Fraseri*. Among those found in Australia but not in Tasmania and with a northern distribution in New Zealand are *Calystegia marginata*, *Bromus arenarius*, *Sparganium subglobosum*, *Cas&ytha paniculata*, and some orchids. These species are mentioned to show that distribution has probably taken place direct across the Tasman Sea, as those plants of southern distribution could not tolerate migration by way of a land bridge in a warmer region. Most species are more generally distributed on both sides of the Tasman Sea than those just mentioned, and this would naturally be the case with plants and animals that have the means of crossing an expanse of ocean.

*The West to East Movement.*—Perhaps the most important movement of organisms migrating by means of wind, currents, or animals in the southern temperate region is that in an easterly direction. It is specially evident in plants where large genera in the continental regions have one or two outliers to the eastward. For instance, many Australian genera containing up to 80 species (*Persoonia*) have a few representatives in New Zealand. *Pliebalium*, *Leptospernum*, *Haloragis*, *Epacris*, and others may be mentioned. Lurge

New Zealand genera like *Hebe* \* and *Coprosma* have one or two species in South America. There are South African genera like *Hypoxis*, *Tetragonia*, *Mesembryanthemum*, *Restio*, *Hypoleuca*, and *Wahlenbergia*, with few species in Australia; while there is a regular trail of Fuegian plants eastwards to the Falklands, South Georgia, and other subantarctic islands.

*The East to West Movement.*—This is very small when compared with that from west to east. Possibly it may be accounted for by occasional bird carriage or upper air currents. Outlying species of the New Zealand genera *Celmisia*, *Ourisia*, *Hebe*, and *Psychophyton* are found in Tasmania. The Australian genera *Hibbertia*, *Keraudrenia*, and *Rulingia* each have one or two species in Madagascar.

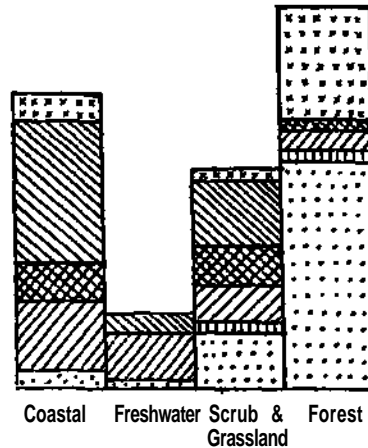
*The Flora and Fauna of Oceanic Islands.*—The study of the plants and animals of islands which on geological evidence appear never to have been united with a larger land area should throw light on the nature of those which are able to cross wide expanses of ocean. The Kermadec Islands may be taken as an instance. According to my own observations (Trans. N.Z. Inst. vol. xliii. p. 524, 1911), these islands have been built up of volcanic materials on a submarine bank. Their plants and animals must therefore all have crossed at least 600 miles of ocean. And it is significant that the bulk of them are related to species found in New Zealand, from which direction come the prevailing winds. The surface currents, as evidenced by logs of New Zealand origin cast up on Sunday Island, flow in the same direction. The vascular plants of the Kermadecs consist of 38 pteridophytes, 20 grasses and sedges (including *Juncus* and *Typha*), 2 orchids, 9 composites, 27 other herbs of which 17 are coastal and none forest, and 18 woody plants of which 14 are forest. Included in the foregoing total are 9 species with succulent fruits. The flora is fragmentary in the sense that there are only one or very few to each genus, and large New Zealand genera, such as *Hebe* and *Coprosma*, are represented in this way. Thus, although most ecological groups occur in the Kermadecs, including trees with succulent fruits which almost certainly depend for their transference on birds, most of the species are ferns, grasses, sedges, composites, and plants of open formations. Of the 114 species, 86 are found in two or more of the adjacent regions of Australia, Polynesia, and New Zealand (see Oliver, Trans. N.Z. Inst. vol. xlii. p. 149, 1910).

The main features of the flora are shown in the diagram (fig. 3). The proportion of coastal plants is much higher than in Lord Howe Island. This, of course, is due to the fact that ocean currents are one of the means of transport, and the land plants depending on occasional means of dispersal number less than half as many as in Lord Howe Island. The coastal plants

\* The following groups are here used in a generic sense, though appearing only as sections of genera in Cheeseman's \* Manual of the New Zealand Flora/ 1906 i—*Hebe*, *Pygmaea* [both = *Veronica*], *Schizeleima* [= *Azorella*], *Edwardaia* [= *Sophora*], *Gymnelaia* [= *Olea*], *Leucogenes* Beauv.

of the Kermadecs include relatively more composites, grasses, and sedges than do those of Lord Howe Island. Freshwater plants are few and mountain plants altogether wanting. The scrub plants of the Kermadecs compare with those of Lord Howe Island, though exhibiting a higher proportion of pteridophytes and composites. Even here the insular character of the flora is evident. But it is in forest plants that the Kermadecs differ essentially from continental forests such as Lord Howe Island and New Zealand. The proportion to the whole flora is high because practically the whole island is under forest. The proportion of species of trees in the forest, which is 43 per cent, in New Zealand and 40 per cent, in Lord Howe Island, falls to 30 per cent, in the Kermadecs, whereas the percentage of pteridophytes in the forest, from 23 in New Zealand and 33 in Lord Howe Island, rises to 60 per cent, in the Kermadecs.

FIG. 3.

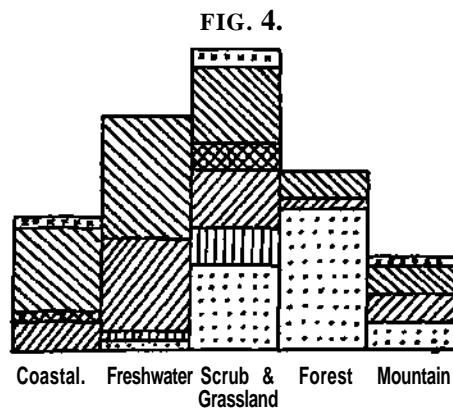


Kermadec Islands Flora.

*Plants common to Australia and New Zealand* (fig. 4).—In the light of results obtained by comparing the floras of oceanic islands like the Kermadecs with continental floras on a large land mass as in 'New Zealand or isolated as on Lord Howe Island, it will be profitable to analyse in a similar way the plants common to New Zealand and other countries. Beginning first with those found in Australia or Tasmania and New Zealand, 320 in number, they may be expressed in diagrammatic form as with the floras already discussed. Coastal plants are in the percentage to the flora here under examination midway between those of New Zealand and Lord Howe Island, with a composition similar to the latter. Freshwater plants occur in large proportion, 25 per cent, of the flora, and consist of nearly half herbs and two-fifths grasses, sedges, and rushes. As has already been pointed out, freshwater plants are apparently easily transported over oceanic areas, so that their fewness on Lord Howe Island and the Kermadecs must be due solely to the fact that the conditions required for their establishment

are there of small extent. Scrub and grassland plants are well represented, and in their composition resemble very closely those of the Kermadees. Forest plants consist of 75 per cent, pteridophytes and the balance herbs, grasses, and sedges. The mountain plants form the smallest group, but this may be explained by the fact that these plants are but a small proportion of the vegetation of south-eastern Australia and Tasmania.

Comparing the plants common to Australia and New Zealand with those of the Kermadees, it will be seen that in those characteristics by which the flora of the Kermadees differs from that of New Zealand, the Australian element in the New Zealand flora differs in a still greater degree. It is indeed more "oceanic" in character than the flora of an oceanic island. This element is of course complex, consisting of species which have reached New Zealand and Australia independently from the Malayan region, species which have reached New Zealand overseas from Australia, and species which have migrated in the reverse direction.

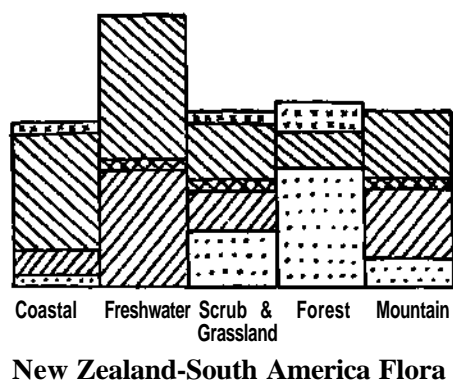


Australia-New Zealand Fauna.

*Plants common to New Zealand and South America* (fig. 5).—Now compare the diagrammatic representation of the 70 species of plants common to New Zealand and South America with that of the 320 common to Australia and New Zealand. In the relative proportions of the five main ecological groups there is an apparent difference owing to the different proportions of the scrub and grassland and mountain groups. But this is due to the latitude in which dispersal takes place, for the scrub and grassland plants of the islands of the southern oceans are mountain plants in New Zealand and are counted as such for the purpose of the diagrams. Now, these form a large proportion of the plants common to New Zealand and South America. Hence, if the scrub and mountain groups be counted as one, the agreement of the diagrams is remarkably close. The percentages for the Australian element in the New Zealand flora are coastal 14, freshwater 25, scrub and grassland 42, forest 19. In the South American element the corresponding figures are 17, 28, 36, and 19. The components of these groups are also in

the two elements quite similar. The most noticeable difference is in the forest group, there being in the South American element two trees. These are *Edwardsia microplylla* and *Coriaria ruscifolia*, both species which at the present day are, there can be little doubt, actually being dispersed, both being found on intermediate islands in the Pacific Ocean. Guppy found that the seeds of *Edwardsia microphylla* germinated after floating for seven months in sea water. *Coriaria ruscifolia* is a plant of open scrubland more than of forest, and bears numerous small succulent fruits which are greedily eaten by birds, though the chances of these being carried by sea-birds would possibly be through sticking to the plumage.

FIG. 5.



Taken as a whole the plants common to New Zealand and South America belong to groups comparable in their characteristics with those common to New Zealand and Australia, and they exhibit in a high degree those features which characterise the floras of oceanic islands. In reality, as will appear in the final part of this paper, the South American element in the New Zealand flora is a complex one, consisting of (1) species which have reached both countries by migration from the Northern Hemisphere, (2) species which have migrated from New Zealand to South America overseas, and (3) species which have migrated from South America to New Zealand overseas. The possibility of any of the species of plants at present common to New Zealand and South America being due to their having crossed by a direct land connection is not here admitted.

#### V. HISTORY OF THE NEW ZEALAND FLORA AND FAUNA.

1. *liesozoic* Floras.—It is insisted by all who study them that the Triassic and Jurassic floras are similar in type throughout the world. They are known from all the continental masses, including Antarctica and New Zealand. As in the earlier floras, therefore, land connections in any definite direction are scarcely indicated. Of the Jurassic plants known in New Zealand six extend to the British Isles, six to India, nine to Australia, and five to Graham Land. The species common to Australia and New Zealand are



given by Arber (N.Z. Geol. Surv. Pal. Bull. No. 6, p. 24, 1917) as follows : *Cladophlebis australis*, *Thinnfeldia lancifolia*, *T. odontopteroides*, *T. Feistmanteli*, *Tamiopteris Daintreei*, *T. crassinervis*, *Coniopteris hymenophylloides*, *Sphenopteris Currani*, *Edocladus conferta*. Of these, *Ectocladus* belongs to the Coniferales; the remainder are fern-like plants and may be seed-bearing; further, of the 45 Mesozoic plants known from New Zealand, six are Cycadofilices, eight Coniferales, and of the 27 fern-like plants included in the remainder many may prove to be seed-bearing. A land connection is therefore demanded with some other portion of the world. Nine species of the New Zealand Mesozoic plants occur in the Upper Triassic (Rhsetic) beds, which would place the land bridge before this time. It might well have occurred during the early Triassic period when on geological evidence, according to Marshall, Park, and others, a break in the faunal succession and a period of orogeny took place. As to the direction in which this land bridge lay, it is not necessary to assume that there was continuous land in temperate regions joining New Zealand and Australia. This is suggested by Arber and mapped by Benson, though Arber states that the comparison of the New Zealand with the Australian and Tasmanian Jurassic floras is more remote than might be anticipated. An extension of land to the north along the route afterwards taken by the Malayan flora would be the probable connection in early Mesozoic times.

2. Malayan Land Connection.—A large proportion of the plants and animals at present living in New Zealand, perhaps the bulk of them, are such as require continuous land connection for their dispersal. Their presence demands that at some period in the past, New Zealand was joined to the other land mass of the globe. Most of these animals and plants are related to species now found in lands to the north, and an explanation of the origin of these must be consistent with the fact of the fundamental differences between the faunas and floras of the south temperate land masses.

*Distribution of Coniferales.*—The distribution of the Australian and New Zealand Coniferales must be considered here. The presence of all may be explained on the assumption of a northern origin. *Araucaria*, *Agathis* (= *Dammara*) *Libocedrus*, *Podocarpus*, and *Phyllocladus* or allied forms all occur in the Cretaceous and Tertiary of Europe and North America. Thus their presence in the Southern land masses is explained by migration along land lines from the north. Knoche (Etude Phytogéogr. lies Baléares, p. 155, 1923) holds this view regarding *Libocedrus* and other genera. The only other New Zealand genus, *Dacrydium*, is represented by several species in the Malayan region and New Caledonia. There are seven species in New Zealand, one in Tasmania, and one in Chile. Fossil species have been described from New South Wales and New Zealand.

The Australian genera include all those in New Zealand except *Libocedrus*,

and, besides these, six genera confined to Australia and Tasmania. *Disehna*, *Microcachys*, and *Athrotaais* are found in Tasmania only, the first two, and *Pherospliwra* with one species in Tasmania and one in New South Wales, are closely related to *Dacrydium*. *Athrotaxis* had allies in the Tertiary of Europe. *Callitris* and its ally *Actinostrobus* are related to African genera. The Ooniferales, being an old order, show a good deal of diversity both in Australia and New Zealand. The congregation of genera in Tasmania perhaps shows, as in the case of New Zealand, some former land extension followed by contraction. The joining up to Australia and subsequent separation would possibly account for this.

*Distribution of FAQUS.*—The history of *Fagus* (including *Notliofagus*) is apparently precisely similar to that of *Araucaria* and *Agathis*. *Notliofagus* differs from *Fagus* only in the smaller size of the flowers and leaves and in the fewer flowers in the male catkins. Some species in Australia [*F. Moorei*] and South America have large leaves. It is found in South America (8), Tasmania and Eastern Australia (3), and New Zealand (4 species and several hybrids), whereas *Fagus* is confined to the north temperate region, including Japan. But *Fagus* has been described from the Upper Cretaceous of Kansas and various Tertiary localities in the United States, British Columbia, Alaska, and Europe. Fossil plants assigned to both *Fagus* and *Notliofagus* have been described from the Oligocene of Graham Land, whilst possibly certain Tertiary plants from Australia and New Zealand may, as Ettingshausen believed, be referred to *Fagus*. It is probable that *Fagus* and *Notliofagus* originated in North America and spread thence east, south, and west. The western moiety passed, via Japan, round the Pacific, reaching Australia and New Zealand. A similar place of origin and routes of dispersal would explain the past and present distribution of *Araucaria* and *Agathis*. But these two genera have become extinct in North America, whereas *Fagus* still persists. If the characters by which *Notliofagus* is separated from *Fagus* be considered primitive, then these two genera exemplify the principle enunciated by Mathew, which states that a group should be most advanced at its point of original dispersal, the most conservative stages being farthest from it. I find that Guppy believes in the northern origin of the New Zealand and South American species of *Fagus* (including *Notliofagus*) (*Plants, Seeds, and Currents in the West Indies and Azores*, p. 326, 1917).

*Upper Cretaceous Flora.*—The late Cretaceous and early Tertiary floras of New Zealand are known only from the determinations of Ettingshausen, whose identifications have not been generally accepted. Many of the plants were referred to northern genera, one was compared with a Greenland species, and the conclusion arrived at that the Tertiary flora of New Zealand was a part of that universal original flora from which all living floras of the globe descend. Ettingshausen supposed that from one part of the Tertiary

flora of New Zealand the present flora was descended, while the other portion became extinct. Probably he has erred on the side of referring too many of the plants to northern genera, though there is nothing inherently improbable in supposing that the first dicotyledonous flora soon became widely distributed, and that the modern floras have differentiated from and displaced it. But such a universal flora would be Mesozoic, not Tertiary.

Ettingshausen referred the Shag Point and related plant beds to the Tertiary, while the Nelson and Westland series (Pakawau, Wangapeka, Reefton, and Grey River) was classed as Cretaceous. This order is now generally reversed. I am indebted to Mr. P. G. Morgan, Director of the New Zealand Geographical Survey, for kindly supplying me with information as to the relative ages of the principal New Zealand plant beds.

Omitting those identifications not founded on leaves, it may be profitable to analyse in a general way the floras described by Ettingshausen. Those which may be considered as of late Cretaceous age consist of 35 species from Shag Point, besides a few from Malvern Hills, Paparoa, Redcliffe Gully, and Murderer's Creek. Of the plants from Shag Point there are two ferns, one of which, said by Ettingshausen to occur also at Dunstan, a mid-Tertiary locality, may be compared with the recent *Dryopteris pennigera*. The gymnosperms comprise two species of *Agathis*, two of *Araucaria*, three of four podocarps and *Sequoia Novce-Zealandice*. Judging by both the present and Tertiary distribution of these genera, northern relationships are indicated. The dicotyledons include eight species with simple entire leaves, a type characteristic of the existing flora. Three species referred to *Ficus*, *Redycarya*, and *Cinnamomum* respectively likewise indicate an alliance with the north. In addition to these there are eleven species having serrated pinnately-veined leaves and two with palmate leaves. These are mainly referred to the Cupulifera, Myricaceae, and Ulmaceae, families which, except for *Nothofagus*, are scarcely characteristic of the present flora. Nothing can be said with any degree of certainty regarding the relationships of these plants, but if Ettingshausen's determinations have any value, they would support the evidence of the gymnosperms for a land connection towards the north. Such a connection would have been during Cretaceous times.

*Eocene Flora.*—The plants referred to the Cretaceous period by Ettingshausen are in reality of later date than the Shag Point fossils, and probably should be classed as Eocene. They consist of leaf and other impressions from the Nelson and Westland districts (Pakawau, Wangapeka, Reefton, Grey River). Four species of ferns are described, of which *Gleichenia obscura* and *Blechnum priscum* show relationships to recent tropical species. A fan palm named *Flabellaria sublongirachis* was present. The gymnosperms consist of *Ginkgodadus Novce-Zealandiui*, a relation of *Phyllocladus*; *Dammara Mantelli*; scarcely distinguishable from *Agathis australis*; and six of the appearance of

podocarps, a group well represented in the living flora of New Zealand. The ferns and gymnosperms, therefore, show unmistakable evidence of relationships with the Malayan element of the New Zealand flora. The dicotyledons include five species with simple entire leaves and five with serrated leaves. These simple leaves are quite characteristic of the present flora of New Zealand. Two leaves named *Ficus similis* and *Cinnamomum Uaastii* belong to types not now found in New Zealand, though, as *Ficus* and *Cryptocarydy* reaching Lord Howe Island. Besides these there are eight species referred to the Cupuliferae and Ulmaceae.

As in the late Cretaceous flora, the evidence of the dicotyledons for determining relationships is inconclusive. The gymnosperms, however, by the absence of *Araucaria* and the presence of *Dammara Mantelli*, *Ginkgoeladus Novce-Zealandia* (S) *Podocarpium pcedacrydioides*, and *Dacrydium cupressinum* show closer relationships with the existing flora of New Zealand, and indicate the same alliances. Whether Tertiary or present gymnospermous floras be compared, therefore, the result is the same—namely, a former northern land extension is proclaimed.

The Tertiary flora of Seymour Island, held by Dusen to be Oligocene, contains the genera *Laurelia*, *Drimys*, *Knightia*, *JSothofagus*, and *Araucaria*. In all these, except *Knightia*, the relationship of the species is with South America. If correctly determined, the leaf referred to *Knightia* is of considerable interest.

*Palaeozealandic Genera.*—Characteristic of New Zealand are many genera and family groups so distinct from any known elsewhere, yet taken together obviously descended from animals and plants that must have existed at a period when there was land connection between the New Zealand area and some other land mass, that they indicate a long period since the connection was severed. The last date that New Zealand formed part of this continent may be taken as some time in the Cretaceous period. It cannot have been later, otherwise land mammals would have entered the New Zealand portion. Cockayne's term Palaeozealandic (Veg. N.Z. p. 315, 1921) might be applied to the genera here listed. His group is of mixed origin according to my views, some of the genera having arisen from the original continental flora, others from species that have afterwards come overseas. •

The continental genera I include under the general heading Malayan element, because they represent the earliest of the higher animals and plants to people the New Zealand area, which I believe would be washed by the ocean except towards the north-west, and in their broader affinities may in most cases be compared with groups of northern origin.

The difference between northern and southern distribution is not so well marked with birds as with plants.

## NORTHERN DISTRIBUTION.

## SOUTHERN DISTRIBUTION.

(a) *Genera with no near relations.*

## Plants.

*Entelea, Melicytus, Alectryon, Astelia,*  
*Lverba, Dactylanthus, Alseuosmia.*

## Plants.

*Corallospartium, Notospartium, Chordospartium, Carmichaelia, Anisotome, Aciphylla, Coxella, Pachycladon, Notholaspi, Stilboca, Myosotidium, Celmisia, Haastia, Leucogeies, Pkormium, Hoheria, Raoulia, Pseudopanax, Simplicia, Psychrophyton, Pleurophyllum.*

## Birds.

*Heterohcha, Callaas, Creation, Turnagra.*

## Birds.

*Bowdleria, Nesolimnias, Cabalus, Notornis, Diaphoropteryx, Apterij, Dinornithide, Xenicus, Traversia, Acanthositta, Nesonctia.*

Mammals—*Mystacops.*

Reptile—*Sphenodon.*

Batrachia—*Liopelma.*

(b) *Genera whose relationships are with Malaya and New Caledonia.*

## Plants.

*Rhabdothamnus, Gymnelcea, Carpodetus, KrUghtia.*

## Plants.

*Siphonidium, Hebe, Coprosma, fygmaa, Chrysobactron.*

## Birds.

*Hemiphaga.*

## Birds.

*Nestor, Gallirallus.*

(c) *Genera whose relationships are with Australia.*

## Birds.

*Miro, Notomystis, Prothemadera.*

## Birds.

*Sceloglaux, Myiomoira, Anthornis, titrigops.*

(d) *Genera whose relationships are with America.*

## Plants.

*Corokia, Loxsoma.*

## Plants.

*Hectorella.*

*The New Zealand Continent.*—Perhaps the outstanding feature of these lists is the large number of genera, including many with a large number of species, with a southern distribution. I take this as indicating a former considerable extension of land about and to the south of South Island, but not necessarily connected with the Antarctic Continent. The date can only be conjectured, but it may be put down as one of the periods when, judging by the geological history of New Zealand, there was a general uplift, perhaps in the Cretaceous and Eocene and again in the late Pliocene periods.

Two biological considerations indicate the continental character of the land. First, there is great diversity of species in the southern genera, species with their areas of distribution overlapping. *Dinornithide, Apterij, Gallirallus, Hebe, Coprosma, Carmichaelia, Aciphylla, Raoulia, Celmisia, and Anisotome* may be mentioned. The crowding together of these species suggests a former wider area where they differentiated. As the land area diminished they have

come together, so that many allied species are found in the locality. Willis interprets these facts as a southern invasion taking place later than a northern one (Ann. Bot. vol. xxxiii. p. 40, 1919). Where this so-called invasion came from we are not told.

Secondly, there are xerophytic characters in many New Zealand plants either in their whole life-history or during a portion of it, in a climate in which at present one would expect only mesophytes. Diels appears to have been the first to suggest that a continental extension was necessary to explain the presence of xerophyte plants in New Zealand, while Cockayne explains the developmental stages of many plants on the same assumption.

As these modifications affect entire genera, it must be presumed that the continental extension which induced their development was at the period when these genera were differentiated. That is, it must be placed early in the Tertiary period, and may therefore be mentioned in connection with the multiplication of species referred to the same cause.

On account of the many lines of evidence, both geological and biological, pointing to a former New Zealand continent, it has been accepted by geologists and biologists alike. The controversial points concern the area it occupied, the time it existed, and the lands it joined. The extension of land above indicated with a northern connection would evidently be sufficient to explain the Malayan basis of the New Zealand fauna and flora and the diversity of life now crowded in a comparatively small area. The early New Zealand continent would be a centre for the development and dispersal of many of the forms of life so characteristic of southern regions, including much of the so-called "Antarctic" flora and fauna. The penguins, shags, and petrels among birds, the Galaxiads among fish, the (Teotrida), and perhaps some marine molluscs, other invertebrates and algae characteristic of southern regions and whose headquarters are in New Zealand, owe their development and distribution to the New Zealand continent, which in former times stretched towards Antarctica, the shore of which would act as a route for dispersal. The only other continent in the same latitude was South America. Australia and Tasmania since the Jurassic period do not appear to have extended much farther south than at present.

*Endemic Species of Malayan and Australian Genera*,—Beside the genera already mentioned there are in New Zealand representatives of many genera which show their greatest area of development in the Malayan region. The species in New Zealand belonging to these genera are all endemic, and their ancestors would enter by the northern land bridge described above. They would, in fact, be the last to enter by such a way. Hence the distribution of these species in New Zealand is for the most part northern.

The principal genera of Angiosperms in the New Zealand flora coming under the present bending are the following *i*—*Aristotelia*, *Drapetes*, *Coriaria*, *Edwardsia*, *Bagnisia*, *Jsothopanax*, *Hedycarya*, *Melicope*, *Litscea*, *Beilschmiedia*,

*Weinmannia*, *Corynocarpus*, *Meryta*, *Schefflera*^ *Gaultheria*, *Pratia*, *Paratrophis*, and *Metrosideros*. I cannot name any birds coining under the present heading j perhaps they change at a quicker rate than do plants. Certain land molluscs, however, such as *Placostylus*, *Rhytida*, and *Paryphanta* may be mentioned here.

Among genera characteristically Australian are some which possibly indicate migration over a continuous land surface. These may have entered by way of Northern Australia, New Caledonia, and Lord Howe Island. The following genera have species in one or more of these places:—\**Olearia*, *Dracophyllum*^ *Hymenanchera*, *Pennantia*, *Exocarpus*, and *Rhipogonum*. Three genera, *Fusanw*, *Quintinia*, and *Ackama*, are confined to the north of New Zealand, while *Plagianthus* is found in the south as well. Thus the Malayan land connection may explain the presence in New Zealand of Australian genera with all endemic species in New Zealand. That such genera as *Dracophyllum* and *Olearia* have been in the New Zealand area a long time is indicated by the large number of species belonging to each in New Zealand and their mainly southern distribution.

3. The Influence of Antarctica.—Perhaps no point concerning the origin and distribution of the New Zealand fauna and flora has given rise to more controversy than the so-called " Antarctic " element. This appears to me to be a mixture of several elements which are considered in different places in this paper. From the genera and species of plants common to New Zealand and South America I have first eliminated those which may be explained by migration from the north overland and from the west overseas. But there remains a residue which seem to demand a more direct land route between New Zealand and South America. By most authorities a land bridge is considered necessary. Thus Hut ton, Benham, Chilton, and Cockayne in New Zealand and Hodley in Australia favour a continental connection. Cheeseman, Schucher, and Schenck, however, on the evidence of the flora think a closer approach of the land areas sufficient.

On account of the relatively small proportion of the New Zealand flora with " Antarctic " affinities and the larger Malayan element, also the contour of the ocean bottom and physical conditions of the Antarctic continent, it seems safe to assume that the most active period of transfer between the South America) and New Zealand floras and faunas must have been at the time of New Zealand's greatest extension in late Mesozoic or early Tertiary times.

The genera of plants which, judging from their present distribution, have their greatest development in South America, and therefore are presumed to have supplied thence the New Zealand representatives, are *Griselinia*, *Ourisia*, *Disearia*, and *Gaya* with a predominantly southern distribution in New Zealand, and *Fuchsia*, *Jovellana*^ *Laurelia*, *Phrygilanthus*, and *Muehlenbeckia* with a more northern or general distribution.

Unfortunately there is nothing known of the early Tertiary Antarctic flora beyond a few Oligocene plants from Graham Land. These are in the main South American types. However, if they are to be taken as an indication of the flora of the Antarctic coast at that time, then it is evident that New Zealand received no more of it than fragments that might have crossed, with the assistance of birds or wind, a small expanse of ocean.

*Griselinia* has four species in Chile and two in New Zealand, the latter species being different in appearance and perhaps belonging to a distinct section of the genus.

*Ourisia* has 19 species in South America, eight in New Zealand, and one in Tasmania. They are mainly plants of mountainous districts, where opportunities for dispersal and establishment are frequent.

*Discaria* has about 18 species in extra-tropical and Andine South America, one in Australia, and one in New Zealand. The two last are closely allied, and *J. discolor* of South America is related to *I. toumatou* of New Zealand.

The New Zealand species of *Gay a* has much larger flowers than any of the 10 South American species.

*Fuchsia* has about 60 species in America from Mexico and Fucgia. Of the three New Zealand species two are closely allied, and the third is local in the northern portion of the Dominion.

Neither of the two species of *Jovellana* in New Zealand is generally distributed. There are two or more species in Chile and Peru.

*Laurelia* has two species in South Chile and one in New Zealand. An extinct species has been described from the Oligocene of Graham Land. The genus is nearly allied to the Australian *Atherosperma*.

*Phrygilanthus* has about 20 species in South America, four in Australia, and two in New Zealand (both rare).

*Muehlenbeckia* has 10 species in South America, seven in Australia (one extending to New Zealand), four others in New Zealand, and one in the Solomon Islands. Of the New Zealand species three are mainly coastal and another occurs in mountain localities.

The species above mentioned show a certain amount of distinctness from the related South American forms, thus indicating the lapse of a long period of time since dispersal took place. They might well be the descendants of stray immigrants that crossed the sea that separated the late Mesozoic or early Tertiary New Zealand continent from Antarctica.

Besides the genera listed above which indicate the derivation of New Zealand species from a South American source, there are a few others which point to migration in the opposite direction.

*Dacrydium*, a genus probably of Malayan origin with its present greatest development in New Zealand, has in Chile a single species, *I. Fonckii*\*, related to *D. laxifolium* of New Zealand.

\* Hutchinson (Kew Bulletin, 1924, p. 54) omits Chile in giving the range of *Dacrydium*.



*Pseudopanax* has five species in New Zealand and two in South Chile.

Perhaps bicentric genera like *Uncinia*, and *Gunnera* with the subgenus *Milligania* confined to New Zealand and Tasmania, and the closely-related subgenus *Misandra* to Chile, Fuegia, and the Falkland Islands, owe their distribution to the former presence of a habitable Antarctic continent.

Discussing the distribution of *Uncinia*, Guppy ('Plants, Seeds, and Currents in the West Indies and Azores,' p. 501, 1917) comes to the conclusion that whilst South America was the original differentiating ground of the genus, New Zealand with a single section has been in later times more vigorous and productive of species. The same author, however (p. 328), thinks that Antarctica has not shared in the history of the plant world since the appearance of Dicotyledons.

The genera enumerated in the preceding paragraphs must be taken as indicating at least an approximation of the New Zealand area to that of Antarctica at some time in the past. It is known that Graham Land supported a land flora as late as the Oligocene period—that is, long after Dicotyledons appeared. But a direct land connection does not appear to be necessary, because of their fragmentary nature and, as has already been pointed out, the species now common to South America and New Zealand form a disbarmonic community.

There does not exist in New Zealand a plant association related to any in South America, all dominant plant species in New Zealand, including *Nothofagus*, being of northern derivation. It may be pointed out too that both the Tertiary, so far as is known, and the recent floras of New Zealand and South America are fundamentally different. The views herein expressed coincide almost exactly with those of Cheeseman (Rep. Aust. Ant. Exp., Bot. vol. vii. pt. 3, p. 53).

*South American—Tasmanian Biological Relations.*—The relationship of the flora of Tasmania to that of South America is far less than that of New Zealand to South America. The New Zealand continent, indeed, seems to have been the source of such plants in the Tasmanian flora as *Aciphylla*, *Psychrophyton*, and *Schizeleima*, and, if so, probably that portion of the South American element in the Tasmanian flora represented by *Gunnera* and *Ourisia* was received by way of the New Zealand continent.

The South American element in the Tasmanian flora is apparently quite small, and that portion which it has not also in common with New Zealand might be explained by drift from the Antarctic continent when its shore supported vegetation and the land extended from Australia to the south of Tasmania.

*Lomatia* has three species in Chile, four are described from the Oligocene of Graham Land, and there are six existing species in Tasmania and Eastern Australia.

*Embothrium* has four species in South America and one in Eastern Australia. *Eucryphia* has two species in Chile, one in Tasmania, and one

in New South Wales. *Prionites* has one species in Fuegia and one in Tasmania. On the other hand, two Chilean species belonging to the genera *Fitzroya* (allied to *Diselma*) and *Orites* may indicate drift from the Tasmanian land extension to the Antarctic shore-Hue.

Much has been made in the past of the relationship of the mammals of South America and Australia, but it has been shown that the South American *Prothylacinus* is a creodont, and that the so-called Diprotodonts of South America are not to be included with the true Australian Diprotodonts, but are in reality a distinct group descended from American Polyprotodonts. Likewise the reptile from the South American Tertiary supposed to be near the Australian *Miolania* has been shown to be quite distinct (Regan, Terra Nova Exp., Zool. vol. i. pt. 1, p. 41, 1914). Finally, Dunn (Amer. Naturalist, vol. lvii. p. 135, 1923) has pointed out that all Amphibian distribution can be explained without recourse to land bridges save connections in the north between the northern land masses.

**4. Species Dispersing Overseas.** *Species dispersing from Australia to New Zealand,* (a) *Endemic New Zealand genera.*—The constant arrival of species of Australian plants in New Zealand overseas during the Tertiary epoch would result in different degrees of endemism according to the time since the species established themselves in New Zealand. Species arriving early and not subject to later additions might become so different as to be classed as distinct genera, others might differentiate into distinct species, but those species that were constantly dispersing individuals to New Zealand or which arrived recently would be identical with Australian ones.

These conditions would result if during past ages there had been a steady easterly movement, including chance arrivals and regular migrants, of plants across the Tasman Sea. The first degree of endemism by which there result in New Zealand distinct genera derived from Australian species may be represented by *Oreostylidium*, *Phyllachne*, *Colensoa*, *Hydatella*, *Sporodanthus*, and *Oreobolus*. Of these, *Phyllachne* and *Oreobolus* have supplied species farther eastward to South America.

(b) *Australian genera with endemic species in New Zealand.*—(1) PLANTS. Included here are a number of fairly large Australian genera with one or few species in New Zealand all or some of which are endemic. The following genera have each one endemic species in New Zealand, the remainder of the species being Australian: *Phebalium* (27 species in Australia), *Epacris* (23), *Persoonia* (60), *Myoporum* (25), *Swainsonia* (32), and *Logania* (18).

*Pimelia* has 80 species in Australia and 12 in New Zealand. They are mostly plants of the coast and mountain scrub. *Haloragis* has 41 species in Australia and Tasmania, of which four extend to New Zealand, and there is an endemic species in New Zealand as well. *Leptospermum* has 25 species in Australia and three in New Zealand (one of which is Australian). *Centrolepis*

has 18 species in Australia, one in New Guinea, and two in New Zealand (one of which is Australian). Other Australian genera with a few species in New Zealand are *Pomaderris*, *Brachycome*, *Cyathodes*, and *Leucopoyon*. Smaller genera that may be mentioned here are *Arthropodium*, *Poranthera*, *Archeria*, and *Forstera*.

In all the above genera, the New Zealand species, judging from the small number represented, may be assumed to be descendants of chance arrivals.

In some cases the distribution suggests that Australian genera supply species to South America direct or by way of New Zealand. Thus *Pratia*, a genus with its headquarters in Australia, but extending to New Guinea and the Himalayas, has three species in New Zealand and one in South America. *Lagenoplwra* has four species in Australia and Tasmania, six in New Zealand, two in Polynesia, and four in South America. *Abrotanella* is very similar in distribution, having three species in Tasmania and Victoria, one in New Guinea, seven in New Zealand, three in South America, and one in Rodriguez. *Ilaloragis erecta* extends to Juan Fernandez. This type of distribution is also shared by the South African genus *Leptocarpus*, which has 11 species in Australia, one in New Zealand, and one in South America.

(2) BIRDS. There are three species of New Zealand birds which seem referable to the category of endemic species differentiated from Australian arrivals—namely, *Cotumix novce-zealandice*, *Casarca variegata*, and *Anthus novce-zealandice*. All are birds of the open country.

(c) *Species identical in Australia and New Zealand: Plants.*—The species of plants common to Australia and New Zealand may be considered in groups according to their distribution beyond these two countries.

It is not contended here that the explanation of the presence in New Zealand of all the species mentioned in the following paragraphs is due to their having migrated from Australia across the Tasian Sea. But it is suggested, that on account of their existing as identical species in the two regions which have been separated during the greater portion of the Tertiary period, and the general eastward movement of plants in the South Temperate Region, the probability is that the bulk of them have made the passage overseas and in the direction west to east.

(1) Cosmopolitan species are here defined as those which extend to the continents of both the Eastern and Western Hemispheres. Besides *ID* species of pteridophytes there are in New Zealand 61 flowering plants of this nature. They consist of 24 grasses, sedges and rushes, five composites, 12 coastal plants, 12 freshwater plants, and eight others (all herbs). It is evident that all these species owe their wide distribution to means of or opportunities for dispersal. To say that they are all or mainly old species as one might infer from Willis's 'Age and Area' hypothesis gives no satisfactory explanation. When independent evidence of the age of these species is forthcoming it should prove or disprove Willis's theory.

(2) There are a number of species (I have listed 25 of flowering plants) which are distributed over Australia, Tasmania, portions of Malaya, Polynesia, and New Zealand, but do not extend to South America. Half of them are grasses and sedges, the remainder herbaceous plants of the coast, fresh water, scrub, or mountain. Forty species of pteridophytes belong to this group, including *Todea Barbara*, found only in South Africa, Australia, Tasmania, and New Zealand.

(3) About 12 species of flowering plants and nine pteridophytes have a southern distribution that would suggest Australia as a starting point, distributing thence to New Zealand and South America. They are of the same general nature as those already mentioned, as far as means and opportunities for dispersal are concerned. They include *Haloragis erecta*, *Myriophyllum elatinoides*, *Geranium sessiliflorum*, *Selliera radicans*, *Gratiola peruviana*, *Carex pumila*, and *Juncus planifolius*. Two species, *Mesembryanthemum cequilaterale* and *Tetragonia erpansa*, have their distribution, in addition to the countries mentioned, recorded as California and Japan respectively, while three have apparently continued their easterly route beyond South America, *Nertera depressa* reaching Tristan d'Acunha, and *Scirpus nodosus* and *Apium prostratum* South Africa.

(4) There are 135 species of flowering plants and 19 pteridophytes confined to Australia, Tasmania, and New Zealand. The flowering plants may be classed under the following systematic and ecological groups:—Grasses, 18 species ; sedges and rushes, 19; orchids, 15 ; composites, 9 ; coastal plants, 11; swamp and other freshwater plants, 23 ; scrub plants, 20 (of which five are woody) ; mountain plants, 14 (of which four are woody) ; forest plants, six (five herbs and *Pomaderris apetala*). This list may be compared with that of the Kermadecs previously mentioned. It has, in fact, the characteristics of the flora of an oceanic island. The inference is that these plants might have crossed the Tasman Sea between Australia and New Zealand by occasional means of transport. A few of them are quite rare in New Zealand.

The New Zealand orchids are mainly of Australian affinity. Of the genera, 14 (including 39 species) may be described as Australian, whilst seven (including 17 species) are mainly Malayan. This distribution would suggest, that the family reached its highest development after the connection between New Zealand and the North was severed, and the species found their way by wind carriage ; hence the preponderance of Australian forms.

The characteristics of the 320 plants common to New Zealand and Australia have already been indicated. They are plants of the shore, lake, swamp, scrub, grassland, and mountain. Taken as a whole they correspond with the type of flora found on oceanic islands, and therefore do not require the hypothesis of a land connection with Australia to explain their presence in New Zealand. In each country those large genera which stamp the flora as distinct from that of other lands and form the bulk of the forest vegetation

have few or no representatives common to the two countries. The plants which are common give no indication whatever of any migration as a whole flora from one country to another.

*Birds.*—There are three species of land birds common to Australia and New Zealand : *Ninox novce-zealamlite*, *Rldpidura flabellifera*, and *Zosterops lateralis*. Of these the last appears to have found its way from Tasmania since New Zealand was settled by Europeans, it having been first noted in the south-west of Otago in 1832. Of birds listed as stragglers—that is, those which have been recorded in New Zealand from a few specimens presumably carried accidentally by storms—there are about 40 species, not counting petrels. They include two land birds (*Graucalus robustus* and *Coleia carunculata*) and seven species of rails and herons, which are inhabitants of fresh water. To these may be added three species of ducks. These last nine species are of interest as indicating how seeds of water plants, grasses, and sedges might be transported. The Grey Duck (*Anas superciliosa*) wanders far ; it and the Harrier (*Circus approximans*) are regular visitors to Sunday Island, 600 miles to the north-east of New Zealand.

*Species dispersing from South America to Tasmania and Australia.*—That there is a continuous stream of migrants originating in South America and moving eastwards is a conclusion that seems evident from the facts of distribution of the plants of the southern portions of Chile and Patagonia. Most of them, one must assume, perish at sea, many reach the Falklands, fewer South Georgia, still fewer the islands of the South Indian Ocean, some Tasmania, and more New Zealand and the islands to the south. It appears to be a question of latitude and distance. Thus the inlands closest to South America are most favoured by these Fuegian plants, whilst of those farthest away the more southern, as the South Island of New Zealand, receive more than those such as Tasmania, which lie slightly farther to the north. Certain South American genera have their farthest eastward range in Tasmania - *Eucryphia*\* *Prionites*, and *Accena* section *Acrobyssinoides*. Others occur in New Zealand as well. Such are *Pernettya* (20 in South America, one in Tasmania, one in New Zealand), *Gentiana* section *Andicola* (50 in South America, one in Tasmania, one in New Zealand), and *Ureomyrrhis*.

*Species dispersing from South America to New Zealand.*—Three Fuegian species of flowering plants are, in the New Zealand region, found only on the islands of the route and east, *Itostkovia majellanica* and *Azorella Selago* have shown their route and origin by their occurrence on intermediate islands, but *Carex Darwinii* outside South America has been found only in the Chatham Islands. Besides these a fern (*Polystichum mohriodes*) is found at the Auckland Islands.

A class of plants not far removed from these so far as distribution is concerned is that consisting of those species occurring in South America, the Subantarctic Islands and mainland of New Zealand, and sometimes

intermediate islands. Such are *Cardamine glacialis*, *Tillcea moschata*, *Carex trifida*, and *Ranunculus acaulis*.

Just as there are New Zealand genera of plants having representatives in South America, so there are South American genera or sections of genera with species in New Zealand. They are fewer, however, and more southern in their New Zealand distribution. Besides those already mentioned as occurring also in Tasmania, there are *Enargea*, *Marsippospermum*, *Carex* sections *Bractiosai* and *Aciculares*, *Geranium* sections *Chilensia* and *Andina*, *Acama* section *Euancistrum*, and *Caltha* section *Psychrophylla*. *Colobanthus* is a genus whose species appear still to be dispersing both from South America and New Zealand. There are 10 species in Andine South America, the Falklands, South Georgia, and Graham Land (*C. crassifolius*). Two of these are found in New Zealand. There are nine species in New Zealand, one in Kerguelon, another in New Amsterdam Island, and a third in Victoria and Tasmania.

*Species dispersing from South Africa.*—It is not here contended that any species have arrived in New Zealand direct from South Africa, but there are several genera which have their centre of dispersal in South Africa and which extend eastward through Australia to New Zealand. Such are *Leptocarpus*, *Ilypolama*, *Hyjwxis*, *Wahlenbergia*, *Tetragonia*, and *Mesembryanthemum*.

*Species dispersing from Polynesia to New Zealand.*—A few species of New Zealand plants may be regarded as having been derived from Polynesia by trans-oceanic migration. *Dianella intermedia*, *Peperomia Urvilliana*, *Macropiper excelsum*, *Pisonia Brunoniana*, and the ferns *Diplazium japonicum*, *Hymenophyllum demissum*, *H. dilatatum*, and *Hymenopteris Thelypteris* are suggested as coming under the present heading, while the orchids of the genera *Earina*^ *Dendrobium*, *Bulbophyllum*, *Gastrodia*, and *Corysanthus* may be descendants of Polynesian immigrants. *Ascarina* is a genus of forest trees that seems capable of crossing wide expanses of ocean. There are three species in New Caledonia and one each in the Philippines, Fiji, Samoa, Tahiti, Raratonga, Kermadecs, and New Zealand. The species from the Kermadecs, Fiji, Samoa, and Raratonga are very closely allied, and related to *A. lucida* of New Zealand.

*Species dispersing from New Zealand to Australia and Tasmania.*—The number of genera having many representatives in New Zealand and with few species in Australia and Tasmania is small compared with those large Australian genera which have one or few species in New Zealand. Furthermore, in the case of the New Zealand genera herein mentioned, the species in Tasmania and Australia are all endemic, showing that transport is quite occasional, if indeed it was not confined to the period when the New Zealand continent extended towards Tasmania. The following New Zealand

genera are considered to have distributed species overseas to westward : *Guinera* subgenus *Milligania* (nine species in New Zealand, one in Tasmania) ; *Azorella*, sect. *Schizeleima* (nine in New Zealand, one in Australia, two in South America); *Ourisia* (19 in South America, eight in New Zealand, one in Tasmania); *Aciphylla* (14 in New Zealand, four in Tasmania and Australia); *Celmisia* (43 in New Zealand, one in S.E. Australia); *P sychrophyton* (seven in New Zealand, one in Tasmania); *Hebe* (90 in New Zealand, two in Tasmania and Eastern Australia). In nearly all the above-mentioned cases the species are mountain plants, and the range on the western side of the Tasman Sea is Tasmania and South-East Australia.

***Species dispersing from New Zealand to Polynesia.***—There are a few genera of Angiosperms whose centre of dispersal is apparently New Zealand and which have one or two species in the Pacific Islands. *Astelia* has one species in Fiji and Samoa, two in the Hawaiian Islands, and one in Tahiti. There is a species of *Oreobolus* recorded from the Hawaiian Islands. *Coprosma* occurs in several islands of the Pacific, as far as Hawaii and Tahiti. *Melicytus ramiflorus* is found in Norfolk Island, the Kermadecs, Eua (Tonga Group), and Fiji. *Coriaria ruscifolia* has reached the Kermadecs, Banks Islands, Fiji, Samoa, Tahiti, and South America ; whilst *Edwardsia microphylla* occurs in Easter Island, Juan Fernandez, South America, and Gough Island. There are also three species of ferns widely distributed in New Zealand but only known elsewhere from one island in the Pacific ; they are ***Lomaria Jiliformis* and *Polystichum Richardi* in Fiji and *Polypodium dictyopteris* in New Hebrides.**

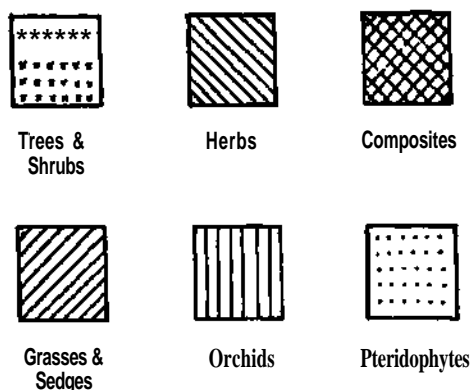
***Species dispersing from New Zealand to South America.***—In considering the origin of the New Zealand element in the South American flora we may omit the ferns, and about 13 others which are cosmopolitan in their distribution, but take into account those species in South America which are closely allied to New Zealand species. The feature of these plants is that most of them belong to genera whose centre of dispersal is apparently New Zealand or Australia. And **this** fact, together with the oceanic character of the species, taken as a whole suggests trans-oceanic migration as the explanation of their present distribution.

Among Australian genera with species in South America identical or allied to species in New Zealand the following may be mentioned:—*Abrotanella*, the three South American species are related to New Zealand ones ; *Gaimardia*, belonging to an Australian family, has one species in Tasmania, one in New Guinea—*G. setacea* in New Zealand and *G. australis* (allied to *G. setacea*) in Fuegia and the Falklands. *Lagenophora*, mainly Australian and New Zealand, has four species in Andine South America, one of which is closely related to *L. pumila* of New Zealand ; *Pratia repens* in Chile, Fuegia, and the Falklands is related to the New Zealand *P. angulata* ;

*Haloragis erecta* of Australia and New Zealand extends to Juan Fernandez; *Leptocarpus* has one species in South America; *JJrosera* section *Psychroplylla* has one species in Tasmania, Australia, and New Zealand, another in New Zealand, and a third in Chile, Fuegia, and the Falklands.

The genera or sections of genera which may be considered of New Zealand origin and having one or a few species in South America are as follows:—*Hebe*, with about 90 species in New Zealand, has *H. elliptica* in the south of South America, Subantarctic Islands, Fuegia, Chile, and the Falklands; whilst *H. salicifolia* of New Zealand has an ally (*H. Fonckii*) in South America. *Coprosma* has one species (*C. triflora*) in Juan Fernandez; *Myosotis* is a North Temperate genus with 24 species in New Zealand, of which one extends to Patagonia and there is another, related to a New Zealand species, in Magellan; *Astelia*, whose centre of dispersal is New Zealand, has one species in Fuegia and the Falklands (*A. pumila*) related to *A. linearis* of New Zealand; *Schizeleima* (section), with nine species in New

FIG. 6.



Explanation of signs used in Figs. 1-5.

Zealand and one in Australia, has two in South America; some small genera with one or few species in New Zealand and one in South America should probably be classed here—*Tetrachondra*, *Phyllachne*, *Donatia*.

There are a few genera which I class as of Malayan origin, but New Zealand is probably the centre from which the South American species have been derived. They are *Aristotelia*, *Nertera*, *Coriaria*, and *Edwardsia*.

Enough has now been given to show that the New Zealand region appears to have been a centre of dispersal for many species that reach as far eastward as South America, and that in their characteristics as regards means of dispersal and occupying habitats giving opportunities for\*dispersal and establishment, the plants common to New Zealand and South America compare with those found on an oceanic island. The conclusion seems to be inevitable that plants have been carried from New Zealand to South America by agencies comparable to those which populate the remote islands



of Polynesia. Exactly what these agents are may require long and close observations in inhospitable climates.

*Circum-austral Species.*—As if showing that distribution is now actually taking place, there are several circum-austral species which, beginning in one of the southern land masses, have completed the circuit of the globe. Such are *Nertera depressa*, *Ranunculus biternatus*, *Tillaa moschata*, *Callitriche antarctica*, *Festuca erecta*, *Edwardsia microphylloa*, *Sciï\*pus nodosus*, *Apium prostratum*, *Agrosfis magellanica*, *Crantzia lineata*, *Oreomyrrhids andicola*, and *Acana adscendens*.

## VI. SUMMARY.

1. There has been a continuous land surface in the New Zealand area since the beginning of the Mesozoic epoch. The early Triassic period appears to have been a time when there was a direct land connection with the north. In the late Triassic a flora consisting of Equisetales, Filicales, and Ginkgoales was common to New Zealand and other southern lands. This flora, together with *Sphenodon*, *Liopelma*, and possibly *Peripatus*, would date from the time of the former northern land connection. «

2. In the later Triassic and in the Jurassic periods there were times when the land was lower and a long series of marine sediments was laid down. Throughout this time there flourished on the land surface a flora including Filicales, Cycadofilices, *Podozamites*, and the early forms of Coniferales. The Jurassic flora was nearly uniform in character throughout the world, extending beyond the Arctic and Antarctic circles.

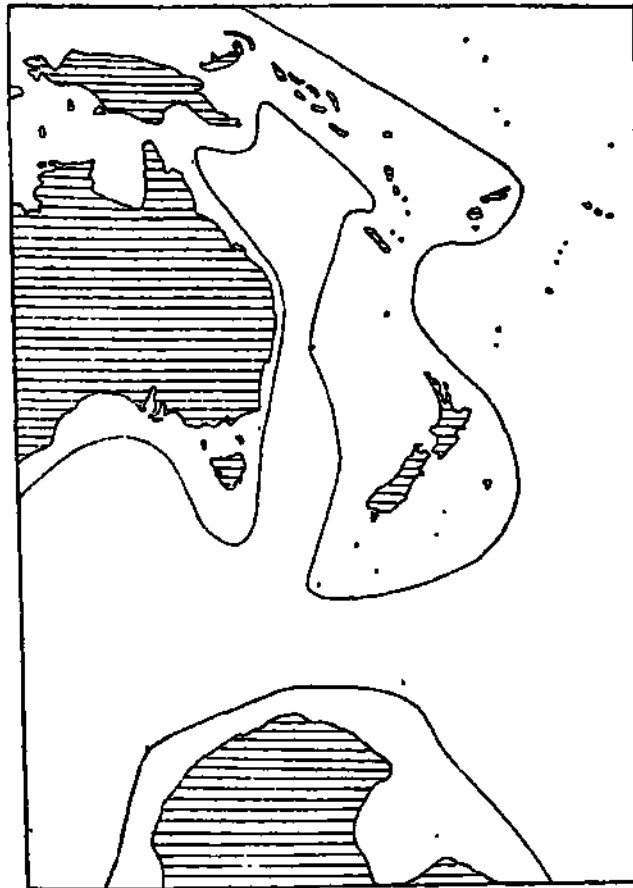
3. In Cretaceous times the land in the New Zealand area was of continental dimensions. It extended to the north so as to connect with New Guinea and North-Eastern Australia, but Western Australia was separated from this continent by an arm of the sea. A sea also intervened between the New Zealand area and Southern Australia (with Tasmania), but the land extended to the south and east so as to include the area of the submarine plateau on which now stands the Auckland, Campbell, Antipodes, and Chatham Islands. The Antarctic continent during this period of elevation no doubt extended farther to the north, approaching perhaps within a few hundred miles of the New Zealand continent. Possibly Macquarie Island was much larger than at present. Mr. H. Hamilton informs me that it contains altered sedimentary rocks of unknown age. According to Thomson (tsept.Austr. Ant. Exp., Zool. vol. iv. p. 60, 1918), the late Jurassic or early Cretaceous was a period of emergent lands all round the Pacific.

The map given by Hedley (Proc. Linn. Soc. N.S.W. vol. xxiv. p. 404, 1899) represents precisely what, judging from the present New Zealand flora and the evidence gradually accumulating of the flora of New Guinea and the islands of the western Pacific, I think necessary for a land connection in the Cretaceous period. The route taken by plants and animals migrating

between New Zealand and the north is as clearly marked by the present distribution of *Agathis* and *Araucaria* as by that of *Placostylus*. The accompanying map, therefore, shows a former land bridge by way of Lord Howe Island, New Caledonia, and the New Hebrides, but I cannot follow Mr. Hedley in his Antarctic connections to the southward.

The Cretaceous period was important in the history of New Zealand, which afterwards was not again united with any other land. The period of land

FIG. 7.



Map of South-west Pacific shewing greatest extension of land required for the dispersal of Spermophytes in late Mesozoic times.

connection with the north must have lasted some time, for two continental floras succeeded one another in the New Zealand area. The first comprised the modern types of Coniferales and Filicales, and the more primitive Angiosperms such as *Nothofagus*. Such genera as *Araucaria*, *Libocedrus*, *Phyllocladus*, and *Nothofagus* appear to have arisen in North America and migrated along the western shore of the Pacific; hence their presence in Australia and New Zealand but absence from Africa. The second flora included the bulk of the ancestors of the Malayan element in the present flora. It included Angiosperms, and with it were associated birds, lizards, insects, and other animals.

Overseas came many animals and plants, some from Australia and Tasmania across the Tasman Sea, and a few from the shores of the Antarctic continent, which supported vegetation.

The New Zealand continent not only received but gave to neighbouring lands some of its productions. It was a centre for the development of many peculiar groups of plants and animals. Shut off from mammals which spread over the world in late Mesozoic and early Tertiary times, its birds filled their place, and a great variety of flightless forms—*Dinornithidae*, *Apteryx*, rails—originated. In the same diversified and extensive land area the plants likewise increased and differentiated along lines adapted to different stations. Hence arose the many species of *Hebe*, *Coprosma*, *Celmisia*, *Olearia*, *Carmichaelia*, and others. It was in the southern portion of the continental area that this new world of life came into existence. Some of these forms wandered back along the land bridge to the north, as *Carmichaelia* and *Phormium*; a few found their way to the southern part of Australia and Tasmania, as *Aciphylla*, *Celmisia*, and *Psychrophyton*; while some even reached the shores of Antarctica, as *Pseudopanax* and perhaps *Dacrydium*.

4. On the breaking down of the land connection to the north the exchange of species between New Zealand and other countries was confined to such as could by chance cross a considerable stretch of ocean. Nevertheless, a great many species of plants both arrived and departed from New Zealand, the lands both receiving and giving being mainly those in the same latitudes—Australia, Tasmania, and South America. A small north and south movement between Polynesia and New Zealand also took place. But in accordance with the means of and opportunities for dispersal this moving population has the characteristics of the inhabitants of truly oceanic islands. The principal sections of the flora received since New Zealand severed its last direct land connection are the orchids and the Australian species.

The flora as it stands today I have endeavoured to represent by means of a diagram (fig. 1). Its derivation for the most part by direct land connection in the north, gives its forests which have nearly half of their species woody plants (some trees and shrubs are included in the Composites), and also a considerable proportion of woody species in the scrub and grassland formations. Continental conditions including diversified mountainous country are shown by the mountain plants equalling the forest plants (30 per cent. each). From Dr. Cockayne's work on the vegetation of New Zealand, I gather that he considers that the mountain plants were mainly differentiated in late Tertiary times. This may be so, but large distinct genera evidently require a longer period for their differentiation.

The paucity of orchids, so abundantly developed in New Guinea and New Caledonia, leads one to conclude that this family reached its highest development after New Zealand's connection with the north had been severed. Composites, which figure so largely in the New Zealand flora (14 per cent.),

are mainly plants of the scrub and grassland areas. Their great development is perhaps a result of continental conditions in both early and late Tertiary times.

In the preparation of this paper I have endeavoured to group the plants and some of the animals of New Zealand according to their place of origin. For the facts of plant distribution I am especially indebted to the works of Clieseman, Cockayne, and Skottsberg. The main groups of animals not dealt with—earthworms, insects, spiders, and Crustacea—have all been used to support the theory of an Antarctic connection in late Mesozoic or early Tertiary times. But opinion is not unanimous on this point, and I venture to predict that, as methods of dispersal among the invertebrates are better known, the arguments for trans-oceanic migration will be strengthened.

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	No. of Species.						Percentages.					
	Coastal.	Freshwater.	Scrub and grassland.	Forest.	Mountain.	Totals.	Coastal.	Freshwater.	Scrub and grassland.	Forest.	Mountain.	Totals.
<i>New Zealand and Stewart Island.</i>												
Trees and shrubs	25	..	52	183	80	340	2	..	4	13	6	25
Herbs	56	70	92	59	174	451	4	5	6	4	12	31
Composites	18	4	48	24	103	197	1	..	4	2	7	14
Grasses, sedges, and rushes.	22	63	62	28	59	234	2	4	4	2	4	16
Orchids	..	5	17	28	5	55	..	..	1	2	..	3
Pteridophytes	3	8	32	97	6	146	..	1	2	7	1	11
	124	150	303	419	427	1423	9	10	21	30	30	100
<i>Lord Howe Island.</i>												
Trees and shrubs	8	..	5	49	..	62	4	..	2	24	..	30
Herbs	24	2	17	20	..	63	12	1	8	10	..	31
Composites	3	..	5	4	..	12	1	..	2	2	..	5
Grasses, sedges, and rushes.	3	5	5	6	..	19	1	2	2	3	..	8
Orchids	..	..	1	3	..	4	..	..	1	1	..	2
Pteridophytes	1	1	4	4*	..	49	1	1	2	20	..	24
	39	8	37	126	..	209	19	4	17	60	..	100
<i>Kermadec Islands.</i>												
Trees and shrubs	3	..	1	14	..	18	3	..	1	12	..	16
Herbs	17	2	8	..	..	27	15	2	7	..	..	24
Composites	4	..	4	1	..	9	4	..	4	1	..	9
Grasses, sedges, and rushes.	8	6	4	2	..	20	7	5	4	2	..	18
Orchids	..	..	1	1	..	2	..	..	1	1	..	2
Pteridophytes	2	1	7	28	..	38	2	1	6	24	..	33
	34	9	25	46	..	114	31	8	23	40	..	102
<i>Australia—New Zealand.</i>												
Trees and shrubs	2	..	5	1	4	12	1	..	2	..	1	4
Herbs	29	40	26	8	11	114	9	13	8	3	3	36
Composites	5	1	10	1	1	16	1	..	3	..	..	4
Grasses, sedges, and rushes.	11	32	18	4	10	75	3	10	6	1	3	23
Orchids	..	3	12	1	..	16	..	1	4	..	..	5
Pteridophytes	1	4	28	46	8	87	..	1	9	15	3	28
	46	80	99	61	34	320	14	25	32	19	10	100
<i>New Zealand—South America.</i>												
Trees and shrubs	1	..	1	2	..	4	1	..	1	3	..	5
Herbs	8	10	4	3	5	30	12	15	6	4	7	44
Composites	..	1	1	..	1	3	..	1	1	..	1	3
Grasses, sedges, and rushes.	2	8	3	..	5	18	3	12	4	..	7	26
Orchids	..	..	..	..	..	..	..	..	..	..	..	..
Pteridophytes	1	..	4	8	2	15	1	..	6	12	3	22
	12	19	13	13	13	70	17	28	18	19	18	100

On the Occurrence of Cavity Parenchyma and Tyloses in Ferns.  
By H. S. HOLDEN, D.Sc, F.L.S., University College, Nottingham.

(With 25 Text-figures.)

[Read 3rd April, 1924.]

THE occurrence of cavity parenchyma in filicinean petioles is familiar to all students of fern anatomy, and there are a number of incidental references to its development in various genera and species scattered through the literature of the group. These references have been collected and amplified by Miss McNichol, who has also made a careful study of its development and maturation in a number of Polypodiaceae and Cyatheaceae, her results being published in the 'Annals of Botany' in 1908 [7]. Miss McNichol defines cavity parenchyma as "a special tissue formed by the conjunctive parenchyma cells of the vascular bundles of the petiole, which replaces the first-formed elements of the wood, sometimes by simply crushing the spiral vessels, but generally by means of tylose-like swellings within the cavity of the vessels." In the second case the formation of tylose-like swellings is followed by their subsequent enlargement, and results in the rupture of the protoxylem elements. Cavity parenchyma thus differs from true tyloses in the fact that its cells cause disruption of the xylem elements which they invade, and also in being confined to the protoxylem. Tyloses, as distinct from cavity parenchyma, are apparently very rare in existing Pteridophyta, and have been recorded only by Conwentz [1], who noted their occurrence in old petioles of *Cyathea insignis*. A second example recorded by Johnson [4] for *Pteridium aquilinum* is open to another interpretation, and will be referred to subsequently.

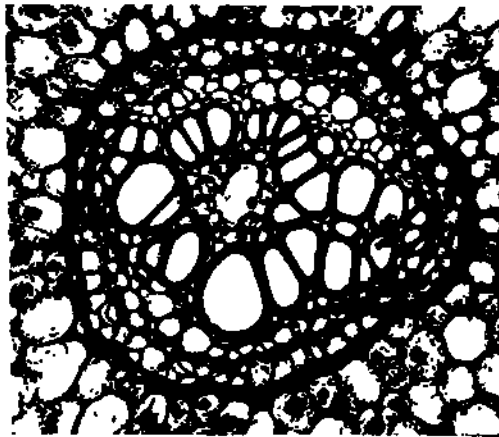
McNichol appears to regard cavity parenchyma as confined to the petiolar strands [7, p. 405], but there is little doubt that it is not uncommonly present in the rhizomes of certain species, this being notably the case in *Pteridium aquilinum*.

As a result of the examination of a considerable amount of material of *Pteridium* rhizome, the following conclusions appear to be reasonably well established:—

1. Cavity parenchyma occurs commonly but not invariably in the rhizomes of *Pteridium aquilinum*.
2. It is frequently well developed in the outer ring of meristeles and may involve the whole of these.
3. It is relatively rare in the inner meristeles and, where it does occur, is less strongly developed than in the outer meristeles.

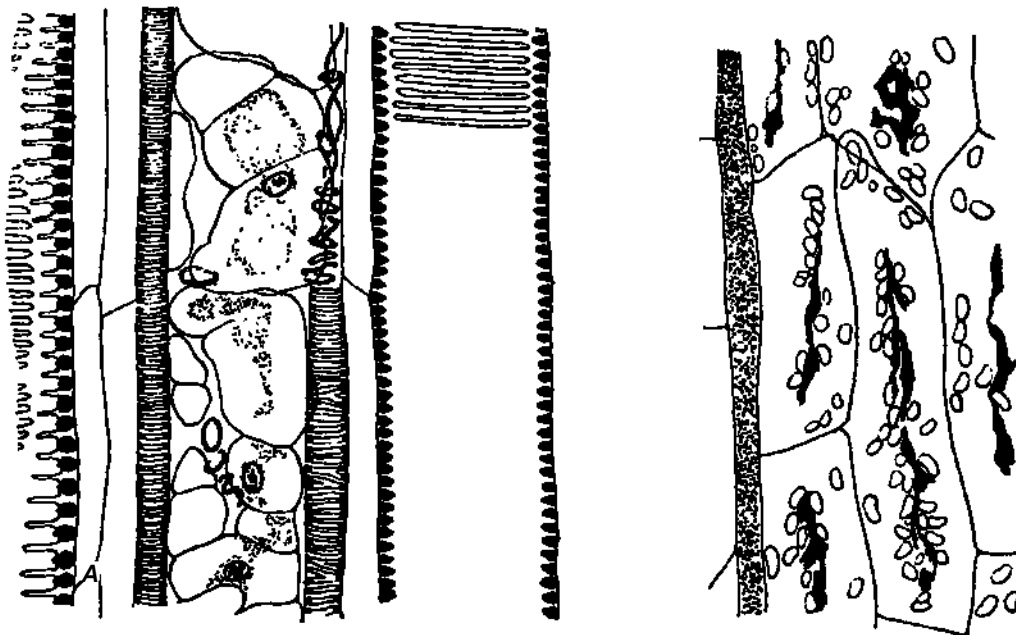
4. Its occurrence shows no evident relation to the proximity of the petiole traces, and cannot be regarded as due to an unusual downward continuation of the cavity parenchyma normally present in the petiole.

FIG. 1.



Photomicrograph of an outer meristele from the rhizome of *Pteridium aquilinum* in transverse section, showing cavity parenchyma replacing the mesarch protoxylem (X 400). From a negative by Professor W. FL Lang, F.R.S.

FIG. 2.



Longitudinal section of a portion of an outer meristele from the rhizome of *Pteridium aquilinum*, showing the cavity parenchyma and the disorganized remnants of the protoxylem (X 600).

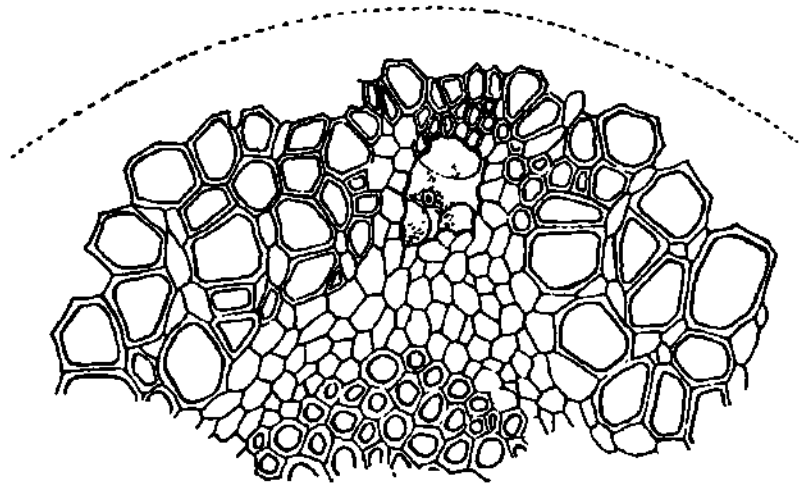
Fig. 1 shows a typical example of its development in an outer rhizome bundle as seen in transverse section, whilst fig. 2 illustrates its characteristic features as seen in longitudinal section. The extremely irregular nature of



the parenchymatous outgrowths and their disruptive effects on the protoxylem are very evident, so that it agrees exactly with that occurring generally in the petiole.

It is almost certain that the case of tylose formation recorded by Johnson [4] is in reality a case of cavity parenchyma formation. McNichol suggests that, in view of its being made from a small detached piece of material, "either it may have been made from a piece of petiole, the tylose-like cells being cavity parenchyma, or that, if cut from the rhizome, it represents an unusual case of continuation of the cavity parenchyma into the rhizome." There is nothing sufficiently characteristic in the tissues shown by Johnson's figures to enable one to identify the specimen with certainty

FIG. 3.



Portion of the outermost solenostele of *Matonia pectinata*, showing cavity parenchyma (X 400).

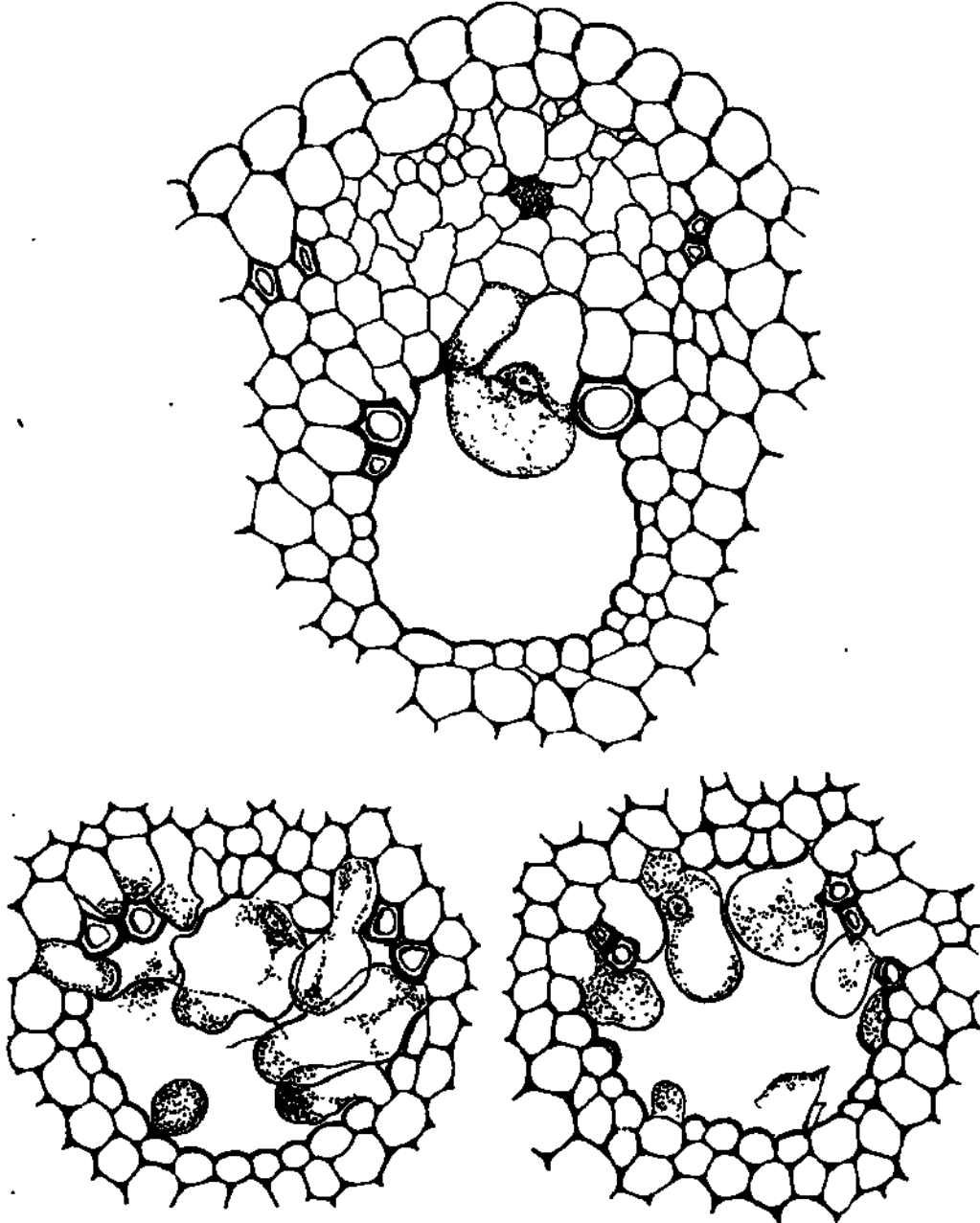
as a rhizome, but, in view of the common development of cavity parenchyma in rhizome strands, his statement that the material was a rhizome may be accepted as correct.

Although an examination of a number of other filicinean rhizomes has been made, only one additional case of cavity parenchyma formation has been discovered. This occurred in *Matonia pectinata* in a mature rhizome possessing three concentric solenosteles, only the outermost one of which was involved (fig. 3). The material from which the sections were obtained was a small fragment of rhizome forming part of the material brought by Tansley from the Malay States. In view of the fact that neither Seward [10] nor Tansley and Lulham [14] refer to the formation of cavity parenchyma in *Matonia pectinata*, it seems probable that its formation in this species is exceptional.

It is interesting to note that ingrowths essentially of the same type as cavity parenchyma may be present in *Equisetum*, Strasburger [12] indeed

mentions the projection into the carinal canal of parenchymatous cells associated with the large connected masses of pitted nodal tracheids, and the same feature is discussed in a more recent paper by Sikes [13]. The case figured below (figs. 4-6) is, however, obviously of a somewhat different

FIGS. 4-6.



FIGS. 4-6. *Equisetum arvense*-Transverse section of carinal canals of rhizome, showing varying degrees of occlusion by tylose-like ingrowths and the development of a cuticle on the cells lining the canal (x 400).

character. The specimen was one of *Equisetum arvense*, the aerial stem of which has been injured and had broken off below ground-level at its junction with the rhizome. In addition, a localized browning of the cortical parenchyma and a partial

collapse of the phloem cells, there has been a development of parenchymatous ingrowths from the cells surrounding the carinal canals. These show a series of stages ranging from slight parenchymatous bulgings into the canal to its complete occlusion by a parenchymatous plug. Particles of soil also occur in the canal, and, where the occlusion is *only* partial, the quiescent cells have developed a well-marked cuticle. The ingrowths here recorded, although they offer an analogy to cavity parenchyma, differ from it in that they extend into a cavity which results from a protoxylem disruption preceding their formation.\* A still closer parallel to the formation of cavity parenchyma is furnished by *Tradescantia virginica*, which has been described in detail by Gravis [2].

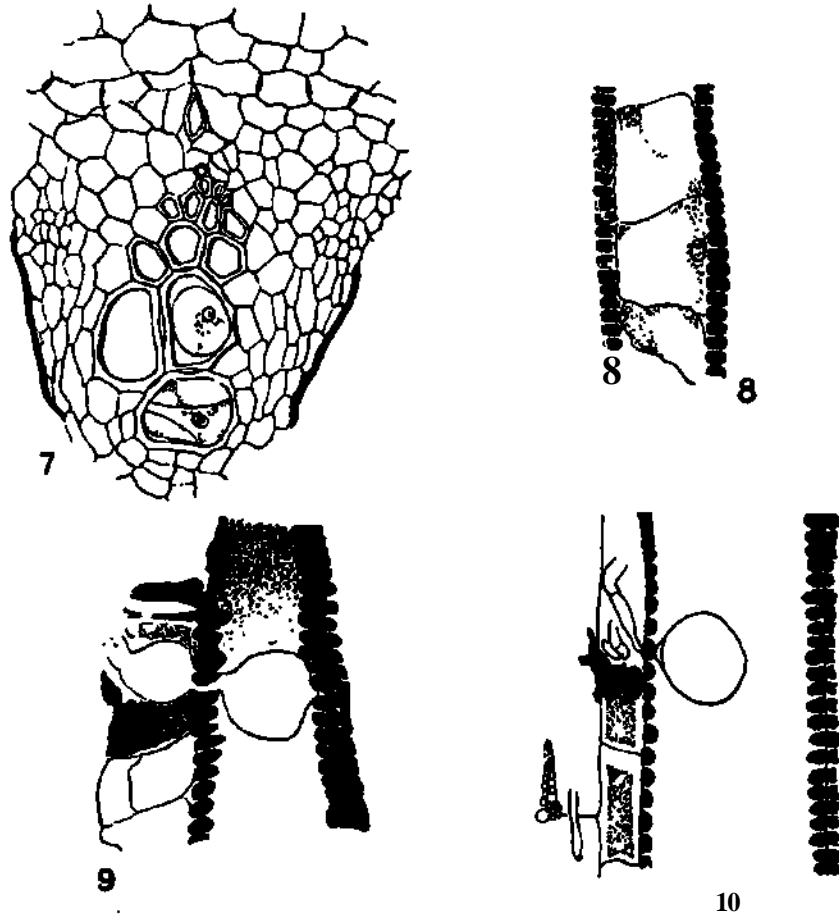
In this plant the xylem of certain of the bundles is defective, and its position is occupied by a lacuna, in which a few annular and spiral elements occur. With the approach of winter the aerial portion of the stem dies down, the internode situated at soil-level undergoing partial decomposition. Immediately below this level the lacunae become occluded by thin-walled outgrowths derived from the small-celled parenchyma surrounding them. These outgrowths, which Gravis regards as strictly comparable with tyloses, penetrate and disorganize the protoxylem elements in precisely the same way as cavity parenchyma.

Whilst the formation of cavity parenchyma as distinct from tyloses is characteristic of existing ferns, it is worthy of note that true tyloses may be formed in response to traumatic stimulus. In the course of an investigation on the roots of the Marattiaceae now in progress, a number of injured roots of *Marattia fraxinea* have been examined. Among the wound reactions shown by these, the closure of the metaxylem tracheids by typical tyloses is frequent, and illustrations of these are given in figs. 7 and 8. A classic instance of the development of tylose-like occlusions of the metaxylem elements in a fossil fern is provided by the petioles of *Ankyropteris corrugata*, in which they are extremely frequent, often completely blocking the whole of the tracheids. They also occur, though generally less abundantly, in the metaxylem of the rhizome and root. These structures were first observed and described by Williamson [16,17,18]. Dealing with them, he says [18, p. 320] :—" I think we shall not risk making any great mistake in concluding we have in them genuine examples of so-called thylosis. The structures so named vary in different examples, but it appears to me that the specimens now described approximate sufficiently closely to the general type of thylosis to be legitimately recognized as examples of it." Williamson's view has received considerable support from Weiss [15], but McNichol, on the other hand, is inclined to regard them as of fungal origin. If they are true tyloses, it is difficult to conceive of the function of an occlusion so widespread that it involves both rhizome and root as well as the petiole, unless it is assumed that

\* I have recently noted a similar condition in a wounded internode of the aerial stem of *Equisetum limosum*.

it furnishes a means of blocking an effete portion of the conducting system. In view of its general occurrence in this species, it can hardly be regarded as pathological. A further difficulty, as McNichol points out, is the irregular nature of the distribution of the occluding growths, a peripheral tracheid being frequently quite free whilst a more centrally placed neighbour may be completely filled. If these occluding growths are derived from the conjunctive parenchyma of the stele, one would anticipate that the peripheral

FIGS. 7-10.



Figs. 7-8. *Marattia fraxinea*—Transverse and longitudinal sections of a small part of an injured root, showing tyloses occluding the metaxylem elements (x 300).

Figs. 9-10. *Ankyropteris corrugata*—Fig. 9. Portion of two adjoining tracheida in longitudinal section, showing a tylose-like swelling passing from one tracheid to another [Nottingham Coll. 261.52]. Fig. 10. Longitudinal section, showing a vesicle-bearing fungal hypha passing from the conjunctive parenchyma into a tracheid [Nottingham Coll. B 24] (both X 400).

tracheids would show the phenomenon more markedly than those further from the margin. It is difficult, too, to conceive a method, apart from direct lateral penetration through contiguous pits from tracheid to tracheid, of invasion of the more centrally placed elements. Such lateral penetration may occur on a relatively small scale in the formation of cavity parenchyma,

and McNichol figures a case in *Nephrolepis* in which three protoxylem elements are successively occluded by an outgrowth from one parent cell. The thickness of sections of fossil plants makes it peculiarly difficult to obtain evidence upon this point, and I have seen only one example in which connection is traceable between the occluding growths of contiguous tracheids. This is illustrated in fig. 9. Such lateral penetration does not in itself, however, serve to determine the nature of the ingrowths, since undoubted fungal hyphae penetrate between the bars of the scalariform tracheids and may form vesicles. A case of this kind is shown in fig. 10, in which the section is unfortunately too thick to show the connection between vesicle and hyphae adequately, although their orientation leaves little doubt as to their union.

Weiss suggests tentatively that their formation may be due to ingrowths from interstitial parenchymatous cells situated at the angles of the tracheids, but there does not seem to be any convincing evidence of the existence of such cells. On the other hand, a definite observation of a liquified tylosis such as that recorded by Weiss cannot be explained away, and lends support to their being regarded as true tyloses difficulties in their method of formation notwithstanding.

It is obviously a difficult matter to obtain conclusive evidence for either opinion, but with a view to collecting further data, a systematic examination has been made of the slides of *A. corrugata* in the Scott and Williamson Collections in the Geological Department of the British Museum, and of the Cash and Hick Collections in the Manchester Museum, as well as of smaller series in the Nottingham and University College (London) Collections.

It soon became apparent that a record of the undoubted fungi occurring in association with *Ankyropteris* would be helpful, and accordingly a survey of the material from this standpoint was first made.

Four fungi which appear to be specifically distinct have been recognized, and three of these may be provisionally included in Seward's genus *Jaeomyces* [11]. They consist of vesicle-bearing hyphae similar to the forms described by Kidston and Lang [5] from the Rhynie cherts, and may be diagnosed briefly as follows:—

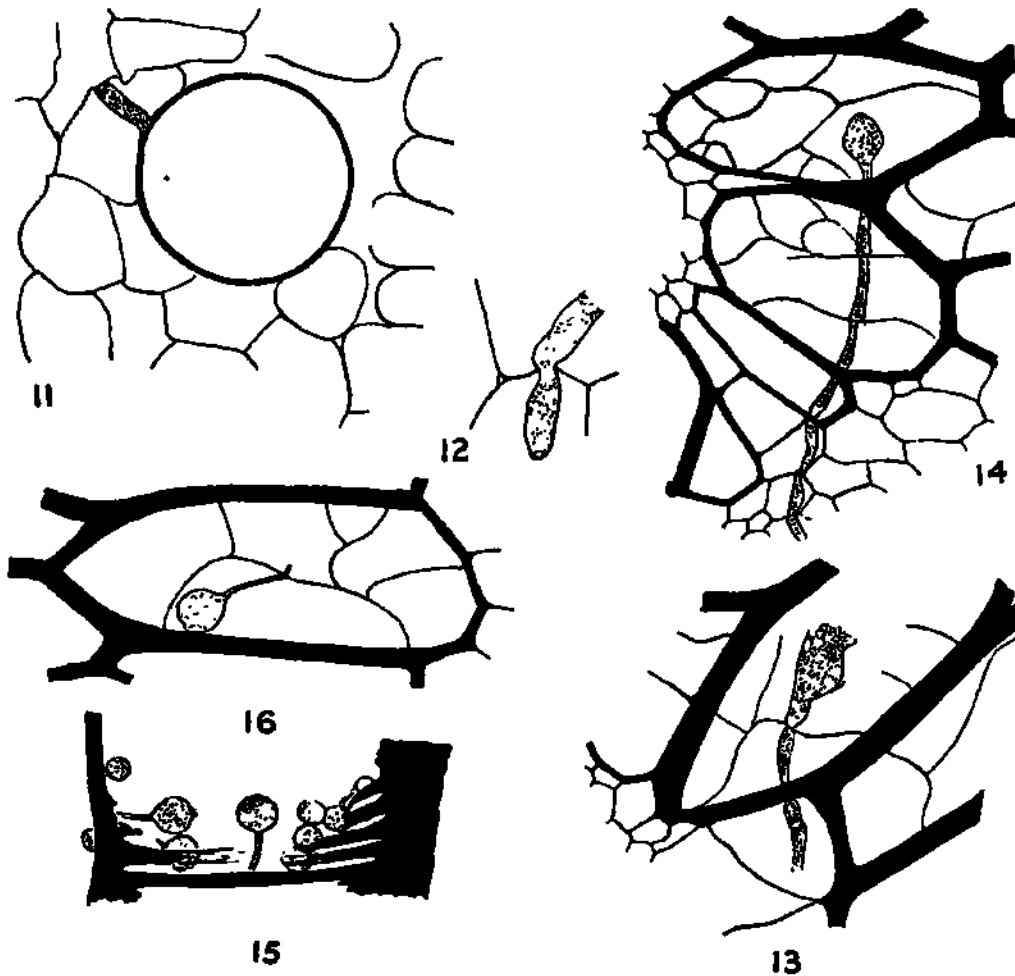
1. *Palaeomyces* a.—Stout non-septate or sparingly septate hyphae, 11-13  $\mu$  in diameter, bearing large terminal vesicles with firm relatively thick walls. The vesicles measured range in diameter from  $130\text{-}160\text{-}\mu$ , with an average diameter, computed from twenty specimens, of  $155\text{-}\mu$ . This fungus is common and generally distributed in all the plant-tissues in the matrix, and was presumably a constituent of the saprophytic soil flora. A vesicle with hypha attached, growing in the inner cortex of *A. corrugata*, is shown in fig. 11 and a hypha passing from one cortical cell to another in fig. 12.

2. *Palaeomyces* b.—Generally non-septate though occasionally frequently septate hyphae, 8-10  $\mu$  in diameter and bearing thin-walled, mostly terminal

vesicles ranging in diameter from 25-70 $\mu$ . This fungus occurs commonly in the parenchymas and tissues and tracheids of both *A. corrugata* and *Botryopteris tridentata*, and is shown in figs. 10, 13, and 14.

3. *Palceomyces* y.—Delicate non-aeptate hyphse, 3-5  $\mu$  in diameter, bearing small thin-walled vesicles 20-30 $\mu$  in diameter. This fungus occurs less

FIGS. 11-16.



Figs. 11-12. *Valaomyces* «-Fig. 11. Typical thick-walled vesicle in the inner cortex of *Ankyroptena corrugata* [Manchester Coll. Q711]. Fig. 12. Hyphae bearing terminal vesicles [Nottingham Coll. 201.69] (both X400).

Figs. 13-14. *Palaomyces* /3-Hyphse bearing terminal vesicles and penetrating several cell walls. Fig. 13 [Nottingham Coll. 261.44]. Fig. 14 [Nottingham Coll. 261.47] (both X400).

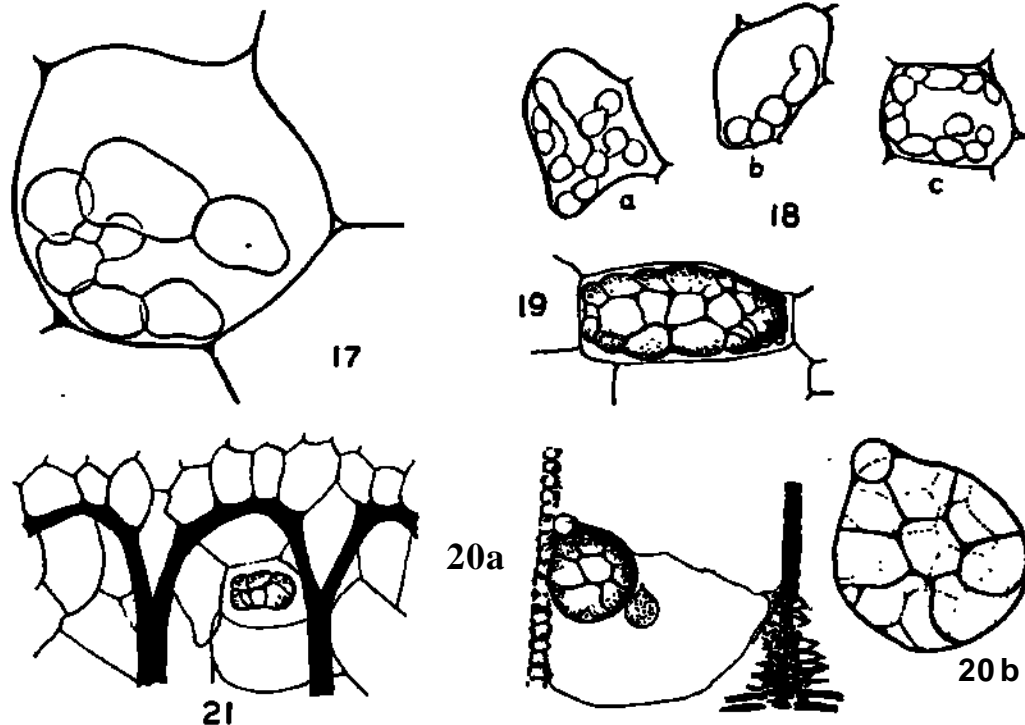
Figs. 15-16. *Palaomyces* 7-Hyph\* bearing terminal vesicles. Fig. 15 is from a partly decayed petiole [Scott Coll. 270T]. Fig. 16 shows a hypha bearing terminal vesicles and penetrating into another cell [Nottingham Coll. 261.76] (both X400).

commonly than the previous type, but in similar situations. There is some evidence that it is a saprophytic form, as it occurs abundantly in the stele and cortex of a much decayed oblique petiole section (Scott Collection, 2707).

A portion of a tracheid from this petiole is shown in fig. 15, whilst other examples are shown in figs. 16 and 20 a.

4. *Haliomyces ankyropteridis*\*.—This fungus stands apart from the remainder, and its distribution suggests the possibility of its being mycorrhizal in nature. It consists of more or less ovoid cells, frequently drawn out into

FIGS. 17- 21.



Figs. 17-21. *Haliomyces ankyropteridis*—Fig. 17. Cell from the rhizome of *Ankyropteris corrugata*, showing typical method of growth of the fungus [Nottingham Coll. L61.69] (X750). Fig. 18 a, b, c. Other examples from the same rhizome (X400). Fig. 19. Assumed resting stage in which the cell-mass takes the shape of the containing cell [Manchester Coll. Q 71 ] (X 400). Fig. 20 a. Resting stage, showing the globular form sometimes assumed. This particular example is lying within a tylose-like growth, and a vesicle of *Palcfomyces* lies close to it [Nottingham Coll. 346.5] (x400). Fig. 20 b: The same, more highly magnified, the dotted lines indicating walls seen at lower foci. Fig. 21. Resting form composed of a small number of cells lying in a tylose-like growth [Nottingham Coll. 261.54] (X400).

a neck-like constriction, where they unite with their fellows. They usually show a grouping and method of branching which is almost yeast-like (figs. 17-18). No hyphae have been detected. They appear to pass into a resting stage in which the individual cells become thick-walled and closely aggregated, and polygonal as a result of mutual pressure. These cell-masses frequently take the shape of the cell in which they occur (fig. 19), but when not occupying the whole of the available space, they may assume a globular

\* Slides 2692 and 2693 in the Scott Collection show this fungus beautifully. They are referred to in Dr. Scott's Catalogue under 2693 as follows:—"Most of the cortical cells in this and other sections are full of granules like starch grains."

form (fig. 20). This fungus appears to be confined to the parenchymatous tissues of *Ankyropteris corrugata*, and is especially abundant in the cortical cells of the rhizome, being present in all the specimens examined. It is always intracellular, and frequently resembles a string of ovoid beads grouped round the periphery of the cell, though other more centrally situated cell-groups are visible at higher and lower foci. It occurs sparingly in the medullary parenchyma of the rhizome and in the inner cortex of the petiole and root. Typical examples are shown in figs. 17-20\*.

Apart from *Palceomyces* a, the relationship of these fungi to the tylose-like growths is one of considerable interest. With regard both to *Palceomyces* 3 and to *Palceomyces* 7, there is some evidence that infection of the tissues of *Ankyropteris corrugata* by their hyphae post-dated the development of the tracheid-occluding growths. This fact is well shown for *Palceomyces* 8 in figs. 13 and 14, which illustrate cases in which it has been possible to trace a single hypha for a considerable length. In fig. 13 the hypha passes from one tracheid into another, and in the second tracheid penetrates the wall separating two adjacent occluding growths, whilst in fig. 14 the hypha passes out of the parenchyma separating the peripheral loop of small tracheids from the main tracheidal mass, through two tracheids, and into a third, piercing a whole series of occluding growths *en route*. The characteristic narrowing of the hypha at the points of cell-wall penetration is a feature which this palaeozoic fungus shares with many existing species, and leaves no reasonable doubt

\*

HALYSIOMYCES, gen. nov.

Fungus endophyticus intracellularis pullulans, e cellulis ovoideis saepe pyriformibus rarius allantoideis compositus, cellulis deinde intersese confertim aggregatis in utraque pressione polygoniis pachydermaticis (quasi sporis perdurantibus), aut massulam subrotundatam aut  $\pm$  irregularem efformantibus aut cellulam matricolem omnino explantibus.

An intracellular budding fungus, consisting of ovoid cells frequently drawn out into a short neck-like constriction at one end, where they are united to an adjacent cell; no hyphae are developed, although occasionally more elongate sausage-shaped cells are produced; apparently possessing a resting stage in which the individual cells become compacted to form a cell-aggregate, become polygonal as a result of mutual pressure, and develop thicker walls; where the host-cell is completely filled the cell-aggregate assumes the shape of that cell, but where this is not the case a rounded or somewhat irregular group may be produced.

H. ANKYROPTERIDIS, n. Sp.

Cellulis aut ovoideis  $35 \times 33$   $\mu$ m  $\times$   $5 \times 8$   $\mu$ m, aut insigniter elongatis  $120 \times 23$   $\mu$ m.

*Hab.* In fossilis filicid *Ankyropteris corrugata* rhizomate, in parenchymate corticis abundans, in parenchymate medullari minus frequens; etiam in parenchymate petioli et radice corticis interni minus frequens.

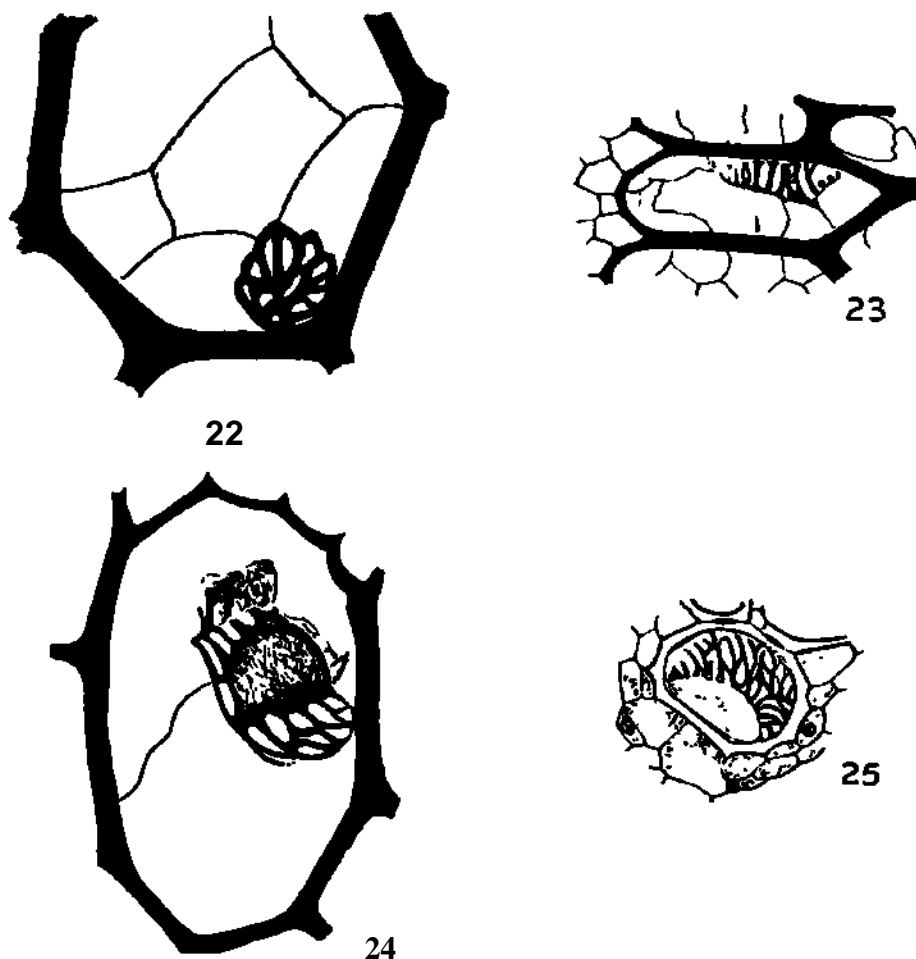
A fungus with the above characters occurring abundantly in the cortical parenchyma of the rhizome of the fossil fern *Ankyropteris corrugata* and less commonly in the parenchyma of the medulla, and in that of the inner cortex of the petiole and root. Dimensions of individual ovoid cells ranging from  $35 \times 33 \mu$ m to  $5 \times 8 \mu$ m; of the exceptionally elongate cells the longest observed measured  $120 \times 23 \mu$ m.

Type-specimen. Slide 2692 [Scott Collection]. This fungus is also exceptionally well shown in Slide 2693 [Scott Collection] and in Slide Q 71 [Manchester University Collection].



that its entry into the tissues occurred subsequent to the formation of the Growths which block the tracheids. Fig. 16 shows a similar condition in the case of *Palceomyces* y. With regard to *Halysiomycetes ankyroptendis* the case is somewhat different. It has been noted in several of the tylose-like ingrowths and always in what is assumed to be the resting condition. In These situations it sometimes consists of two or three cells only (fig. 21). If true hyphae do not occur in this fungus, it seems probable that its presence in

FIGS. 22-25.



Figs. 22 & 24. Fig. 22± *Anhyropteris corrugata*-Lignified "tylose", described by Weiss [Manchester Coll. R 448]. Fig. 23. Similar specimen in the Nottingham Coll. [26174]. Fig. 24. Similar specimen in the Scott Coll. [2714]. Fig. 25. Lignified tylose in a metaxylem tracheid of the root of *Marattiafraxinea*.

the tracheids is due to its being carried into them by the growths in which it occurs, so that its presence provides indirect support for the view which regards the latter as true tyloses.

This view receives further support from the discovery of other undoubted examples of lignified cells within the tracheids in addition to that described by Weiss. The additional examples are ten in number, six being in the Nottingham Collection, three in the Scott Collection, and one in the University College (London) Collection. The case described by Weiss (R448,

Hick Coll.) \* is present in a petiole cut near its base before the characteristic peripheral loops have developed. It consists of a small, more or less discoid structure situated in the angle of one of the larger tracheids, and shows a reticulate type of thickening which at its free margin has a curious crenated appearance (fig. 22). The specimens in the Nottingham Collection are not so heavily thickened, and in most of them the lignification is spiral in type, with occasional cross-connections suggesting a transition to the reticulate condition (fig. 23): one, however, is reticulate. Of those in the Scott Collection one (Slide 2714) occurs in a petiole which is still united by its cortex to the parent rhizome and, like that in the Manchester slide, is reticulate in type (fig. 24). The most interesting specimen in this collection, however, is one occurring in a longitudinal section of a stem (Slide 2692) in which a vertical row of lignified tyloses is present. The University College specimen (Slide K 610) is also a longitudinal section of a stem and shows two examples of tracheid occlusion by lignified tyloses. In the tyloses occurring in the roots of *Marattia fraxinea*, to which reference has been made earlier, lignification is not uncommon (fig. 25), and it is interesting to note that both spiral and reticulate types of thickening occur as well as transitional forms, so that in this respect they are closely comparable with those occurring in *Ankyropteris cormigata*. A crenation of the free margin similar to that shown by Weiss's specimen is not infrequent in *Marattia*, but by careful focussing it is generally possible in the recent examples to distinguish the delicate cellulose wall of the parent cell. It seems probable that, in the case of the fossil specimen, the preservation was not sufficiently perfect to enable us to distinguish this feature. Since the occurrence of lignified fungal hyphae is unknown, it is evident that the balance of the available evidence supports the view that the occluding growths in the tracheids of *Ankyropteris corrugata* are true tyloses, although some of the difficulties presented by their distribution remain unsolved.

#### *Summary.*

1. Ovary parenchyma, though generally confined to the petiolar protoxylem area\* in the Filicales, frequently occurs in similar areas in the rhizomes of *Pteridium aquilinum*.
2. In this species it occurs chiefly in the outer ring of meristeles, and is only found occasionally in the inner system.
3. It also occurs sometimes in the rhizome of *Matonia pectinata*.
4. An analogous type of parenchymatous ingrowth may be formed in the internodal carinal canals of the rhizome of *Equisetum arvense* as a result of wounding.
5. True tyloses, resulting in the occlusion of the metaxylem, occur in wounded roots of *Marattia fraxinea*. These may become lignified.

\* The catalogue number of this slide is erroneously given as R 447 by Weiss [15].

6. The evidence as to the nature of the growths occluding the metaxylem elements in the fossil fern *Ankyropteris corrugata* is reviewed, and is held to support the view that they are true tyloses.

I should like to express my thanks to the Keeper of the Geological Department, British Museum, for permission to study the slides in the Williamson and Scott Collections ; to Mr. W. N. Edwards, for many kindnesses whilst working at the British Museum ; and to Professor F. E. Weiss and Professor F. W. Oliver, for the loan of slides of which they have charge. To Mr. J. Ramsbottom and Mr. F. T. Brooks I am indebted for information with regard to the behaviour of fungal hyphae and also to the former for the Latin diagnosis of *Halysiomyces*.

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- <sup>17</sup>\_\_\_\_\_ *Ibid*, clxviii. 1880.
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Some Critical Species of *Marrubium* and *Ballota*, and a Note on  
*Colehieum montanum* Linn. By O. O. LACAITA, F.L.S.

(PLATE 3 & 3 and 3 Text-figures.)

[Read 8th January, 1925.]

IN the 'Species Plantarum' of 1753, and again in the second edition without material alteration, Linnaeus does no more than repeat, in most cases *tolidem verbis*, the diagnoses of the species of *Marrubium* that he had already published in the 'Hortus Cliffortianus' of 1737. Several of the synonyms and part of the observations are omitted in the latter work, presumably for the sake of brevity. One or two fresh synonyms are introduced, but the only material changes are the subdivision of *HI. peregrinum* in («) and (£), and of Hort. Cliff. no. 8 into two species, *Pmulo-Hctanuis* and *acetabulosum*. It follows that in this genus, with one exception mentioned hereafter, the specimens of the Clifford herbarium carry more weight than those of Linn. in elucidating the author's meaning. They are not unfrequently in conflict. In this case, as in sundry others, Linnaeus seems to have forgotten in 1753 his earlier knowledge of plants described in Hort. Cliff., of which he no longer possessed the specimens.

In Sp. Pl. he enumerates four species "*calycibus 5-dentatis*" and five "*calycibus 10-dentatis*." Of the latter all but *Marrubium vulgare* have since been transferred to the genus *Ballota*, and none of them will come up for remark except *M. hispanicum*. Of those with five calyx-teeth, the first, *M. Alyou*, is represented in both herbaria and raises no problems, the remaining three have long caused perplexity, due in varying degree to lack of specimens, to similarity of forms, to slips of the pen or of the printer, and to disagreement between text and specimens.

## I.

### MARRUBIUM CANDIDISSIMUM.

This name has always been applied in modern times—though wrongly, as Dr. Oegen has pointed out in a recent paper « Ueber *Marrubium candidissimum* L. » in Bot. Közlem. xx. (1922)—to a well-known species found on both sides of the Adriatic, with white, almost silvery foliage, whorls of many flowers, and bracts as long as or longer than the tube of the calyx, whose teeth are longer and more divergent in fruit than in any other species here spoken of. The earliest distinctive name for this plant » certainly, as Dr. Oegen declares, *M. incanum* Desr. in Diet. Encyc. m. p. 716 (1789).

The identity of Desrousseaux's species is conclusively established by his description, his reference to Hort. Elth. fig. 215, and the specimen labelled *incanum* in Herb. Lamarck, which I have inspected\*. It will appear directly that Linnaeus knew, or ought to have known, this plant, but he included it in his composite *peregrinum*, and did not refer it to his *candidissimum*.

What then did he mean by *randidissimum*? All that he says in Sp. Pl. is to quote his own diagnosis of no. 4 in Hort. Cliff., *M. foliis subovatis lanatis, mihi emarginato-crenatis denticulis calycinis subulatis*, and to refer to *J. album candidissimum et villosum* Tourn. Cor. p. 12 as a synonym. Unfortunately Tournefort's plant is untraceable, so the only help this synonym gives us is to establish that *candidissimum* is not a European but an Oriental species, like all the others comprised in the 1356 enumerated in the "Orbollarium in quo praesentia in Orientalibus Regionibus observata recensentur."

In Tournefort's herbarium at Paris the name only occurs on the label of specimen no. 1290, which reads: "*Atarralum album yrcpnm foliis ad basin acutis; Marrubium album candidissimum et villosum* Coroll. List." The plant on the sheet, and a similar one on a second sheet which bears no label, is only a form of *M. vulgare*, with characteristically uncinately calyx-teeth, ten in number. It is less tomentose, and with less rugose leaves than usual in *vulgare*; the leaves being cuneate rather than ovate at the base. Similar specimens occur in herbaria from very different parts of the area of the species; for instance, Tossia in Asia Minor, Palermo, Morocco, the Swiss Valais, Södermanland in Sweden, and Hoboken near New York. Now either, as seems probable, the words *M. album candidissimum et villosum* have no business on the label of this specimen, or else, if this is really what Tournefort meant by that name, it cannot possibly throw any light on a species which Linnaeus has placed among those with only five calyx-teeth, those teeth being not uncinately but subulate.

We are therefore thrown back on the diagnosis, on the specimens, and on a supplementary reference in Syst. ed. xii. p. 316 (1767) to a figure in the 'Hortus Elthamensis.' The diagnosis first appears in Hort. Cliff., and is merely repeated in Sp. Pl. with the slight modification of *dentibus subulatis* instead of *setaceis*, which for the moment we may assume to have been a slip of the author's pen or of his scribe. If, therefore, we should find that the specimens in Herb. Hort. Cliff. differ from the corresponding ones in Herb. Linn., it is obviously on the plant from Clifford's garden, and not on specimens acquired at a much later date, that Linnaeus based his diagnosis.

\* There is another specimen of the same in Herb. Lamarck, labelled *candidissimum*, although Desrousseaux catalogues *M. candidissimum* Linn., as unknown to him. It follows that Lamarck's herbarium is not always to be relied on for identification of names in the Diet. Kncyc.

f *Setaceis* in Hort. Cliff. See p. 159 as to this alteration.

Now, what do we find in Herb. Hort. Cliff.? Two specimens, of which -Pis.2 A3 show photographic reproductions, labelled respectively *Marrubium folio rotundo candidissimo* and *Marrubium folio candidissimo orbiculari*. These have been subsequently labelled by some post-Linnean hand *candidissimum* and *candidissimum* (cancelled by a stroke of the pen) *peregrinum*, the last a bad shot to which we need pay no attention. The original phrase-names are those of *Marrubium* no. 2 and *Marrubium* no. 8 in Boerhaave's Hort. Lugd. pp. 136, 137 (1720), to both of which Boerhaave has set the query, "An *Marrubium album candidissimum et villosum* T. Cor.?" Both of the phrases are quoted in Hort. Cliff., though omitted in Sp. PL, as synonyms of *Marrubium* no. 4. It looks as if these plants grown for Clifford had been received from the Leyden gardens, the source from which Dillenius tells us that they came to Eltham, and that Linnaeus, when compiling his account of Hort. Cliff., had copied the Tournefort synonym from Boerhaave without inquiry and omitted the interrogation. We shall see directly that there is reason for holding that synonymy to be wrong.

Now examine the specimens themselves; after very careful inspection I think they may both be determined as garden-grown examples of *Marrubium ylobosum* Monthr. & Auch., a species from Asia Minor described in Bentham's "Labiatae orientales herbarii Montbretiani" Ann. Sci. Nat. sér. 2, vi. p. 53 (1836), and very nearly allied to *M. astracanicum* Jacq. Linnaeus's diagnosis, as far as it goes, agrees much better with these specimens and with others of *globosum* \* than with *M. incanum*, the leaves of which could not rightly be called *subovata apice emarginato-crenata*. To clear the ground we may point out that *M. album candidissimum et villosum* cannot be *incanum* Desr., because Herb. Tourn. no. 1285, which obviously is *incanum*, bears the label *M. album latifolium peregrinum* C. B. P., an interpretation of Bauhin's name to which Linnaeus also shows some partiality. For a guess as to the meaning of Tournefort's *album candidissimum et villosum* see below under *M. circinnatum*.

So far we may say that *Marrubium* no. 4 of Hort. Cliff, and the two specimens representing it are *M. globosum*. Now, if at a later date Linnaeus, without materially altering his diagnosis, laid in his herbarium a totally different plant for his *candidissimum*, that would merely amount to a false determination of an individual specimen, not to a complete change in the connotation of a specific name. This is just what he has done, for in Herb. Linn, on the sheet now no. 3 there lies an unmistakable *M. incanum*, sine

\* The examples of *M. globosum* on which I have relied for comparison are: (1) Aucher-Eloy, no. 1787, from Ak-Dagh in the Taurus; (2) C. Pinard, anno 1843, from Caria; (3) Uoissier, from M. Cndmus above Gheyra in Caria; (4) Bourgeny, from Ak-Dagh in Lycia, distributed under the wrong name of *micranthum*; (5) Pichler, from Bei-Dagh in Lycia; (6) Bornmiiller, pi. exs. Anatoli® or anno 1889, no. 607, from Amasia; (7) Siehe, aimo \*895, no. 215, from Cilicia, wrongly named *M. heterodon* in Herb. KVw.

loco, alongside of a smaller piece of a very dissimilar plant, *M. supinum* Linn.\* There is only one label for both, written by Linnaeus himself, which at first read *peregrinum*, but this word was subsequently cancelled by a stroke of the pen, and *candidissimum* substituted, also in Linnaeus's hand. Such a muddled sheet cannot possibly overrule the diagnosis of *candidissimum* with which both pieces disagree. Moreover, there is pinned (when? by whom?) to that sheet another, no. 4, which is one of those originally belonging to Hort. Cliff. but later cut down to the size of the sheets in Herb. Linn. The specimen is so arranged as to appear to grow out of the well-known flowerpot design of Herb. Hort. Oliff. It is very perplexing at first sight, for though it looks like the other two Hort. Cliff. specimens already mentioned, the basal leaves are something totally different. There is no writing on the face of the sheet except the one word *Marrubium* at the top, but on the back we read " *Sideritis cretica tomentosa candidissima, fiore luteo* T. cor. 12. *Stachys minor italicu* O. B. P. 236 et *Pilosella syriaca* C. B. P. 262." On more careful inspection it becomes evident that the stem and upper part are not attached to the root-leaves, and that while the upper part is in fact a *Marrubium*, the root-leaves are indeed those of *Sideritis syriaca* Linn. !! What are we to say then? That *Marrubium candidissimum* is *M. incanum* Desr. on the sole evidence of sheet no. 3? Surely not; it is too clearly an Oriental species, in spite of the impossibility of ascertaining the real meaning of the Tournefort synonym.

There is yet more evidence: in Syst. xii. p. 396 (1767) Linnaeus quotes for *M. peregrinum* a figure in Hort. Elth. (1732) as 211, tab. 175, f. 214, and for *M. candidissimum* 21b, tab. 174, f. 214. Here there are two misprints, repeated in later editions: tab. 175 does not show a *Marrubium* but *Ilorminum*. In both cases tab. 174 is meant; but then fig. 214 is quoted twice and Hg. 215 is omitted. Fortunately I have been able, with the assistance of Dr. Daydon Jackson, to find the clue to what Linnaeus intended to say. The plate in question, tab. 174, contains two figures, 214 on the left, 215 on the right. In his own copy of Hort. Elth. Linnaeus wrote *candidissimum* below the left-hand fig. 214 and *peregrinum* below the right-hand fig. 215. That copy can no longer be traced; it was once in Smith's possession, but he sold it to Dr. Woodward and retained his own copy, now in the library of the Linnean Society, "*prout optimum*" as he wrote in the margin of an old MS. catalogue now belonging to the Society. Very wisely, before parting with Linnaeus's copy, he transcribed the above identification at the foot of the plate in the copy now with the Society. This MS. note

\* It is surprising to find this particular confusion with *supinum* among Linnean specimens, though it is one often made by earlier authors, as by Dillenius Hort. Elth. in the synonymy for his fig. 215.

t Visiani, Fl. Dalm. ii. p. 217, though unacquainted with this MS. note of identification, points out that fig. 215 is precisely the *candidissimum* of the 'Flora Dalmatica,' i. e. *incanum* Desr., and that fig. 214, quoted by Linnaeus for *candidissimum*, does not represent either *incanum* or *peregrinum*. We may ignore the absurd mixture of synonyms which Dillenius himself quotes for fig. 215.

of Linnaeus proves conclusively that at the date when it was written he regarded *incanum* as referable to his *peregrinum*, for fig. 215 is precisely Desrousseaux's species, whereas fig. 214 is obviously not *incanum*, but to my eyes appears to be *globosum*, or at any rate the Hort. Cliff, plant which I have determined as such. The conclusion is quite clear ; the name *candidissimum* Linn, cannot be used for the Adriatic *incanum* Desr., but if the identification of the Hort. Cliff, specimens with *globosum* be accepted, it would take the place of that name.

There are still some minutiae to notice. As already mentioned, the phrase *dentiadis setaceis* of Horfc. Cliff, is altered to *denticulis snbulatis* in Sp. PI. for *M. candidissimum*, but on the other hand *M. peregrinum* becomes *denticulis xetaceisj* whereas in Hort. Cliff, it was *denticulis subulatis*. As in Sp. PI. Linnaeus only quoted the diagnoses from Hort. Cliff., it is not improbable that the exchange of the two words subulate and setaceous WHS unintentional, and is due to a slip of some copyist. That no change was intended is, I think, supported by the observation in Hort, Cliff, under no. 4, "*ad antecedentem proxime accedit, sed folia rrassiora et denies setacei rigidiusculi.*" So here we have the *denies setacei* twice repeated. The descriptionH of later authors, e.g. Bentham and Boissier, assign to *peregrinum* calyx-teeth with a wider base (i. f. *svbulati* not *setacei*) than in other nearly allied species. This is in agreement with Hort. Cliff., and an additional reason for thinking that the alteration in Sp. PI. was accidental.

The habitat for *candidissimum* is given in Hort. Cliff, as "*Creta, ut fertur,*" in Sp. PL as "*Cret?i ?*" A very usual guess in those days as to the source of plants of unknown origin. As a matter of fact, neither *incanum* nor *globosum* is found in the island, though possibly *peregrinum* in the form of *creticum* Mill, grows there.

## II.

### MARRUBNJM PEREGRINUM.

*Marrulnum peregrinum* Linn, is a composite species in which Linnaeus distinguishes an (a) synonymised with *M. alterum pannonicum* Clus. and *M. album latifolium peregrinum* C. B. P., and a (£) identical with *M. album angustifolium peregrinum* C B. P. and *M. creticum* Dalech., which afterwards became *M. creticum* Mill.

It will be convenient to take (*ft*) first, as its identity is so well known. It is *M. peregrinum* Jacq. Fl. Austr. tab. 160, a species which ranges from Prussian Suxony across central Europe to Gréece, and possibly to Crete. It grows very plentifully near Vienna, whence it has been distributed in Fl. Exsicc. Austr. Hung. no. 171. This is the plant usually undeMood by continental botanists under the name *peregrinum*, though Reichenbach, Ic. Crit. iv. p. 75 (with an admirable figure, no. 4(U, agreeing with Jacquin's plate), and Celakovsky, Prodr. FL Böhm. p. 84J, prefer to use the name *creticum* Mill. It first appears in Penn & Lobel's Stirp. Adv. Nov. p. 222 (1576), with a Plantinus woodcut, as *Marrubium creticum angustiore folio*,



*odore gratiore*, quoted by C. Bauhin as synonymous with his *M. album angustifolium peregrinum*. The same woodcut reappears in Dalechamp, Hist. PL p. 692, as *AL creticum* Pense. The claim of this plant to grow in Crete is doubtful\*. Smith in Fl. Gr. Prodr. certainly records it for the island as *AL creticum* W., *M. peregrinum* # Linn. On the other hand it has never been found there by any later collector than Sibthorp. The specimen in Sibthorp's herbarium—precisely the species of which we are speaking—is *sine loco*, and whatever evidence Smith may have possessed that it really came from Crete and not from the mainland of Greece, is now lost. Smith often made mistakes as to the origin of Sibthorp's specimens. This one agrees perfectly with Heldreich's Herb. Grsec. Norm. no. (50 from Parnassus. Both are remarkable for their very small bracteoles, shorter than in the Austrian type. The Hort. Cliff, specimen of *AL album angustifolium peregrinum* belongs to this *peregrinum* /8, so does the *At. creticum* in herb. Lamarck, but those of herb. Tournefort which should represent it do not. Herb. Linn, also contains a surprise or two under the name *peregrinum*, which will be mentioned below. Meanwhile there seems to be no sufficient reason for disturbing the current use of "*peregrinum* Linn." for this species, although it is a /3. In this case to attempt to restrict the employment of the name to a would lead to irreconcilable differences of opinion.

It is on turning to *peregrinum* (a) that we encounter serious difficulties. Is this just the plant of Clusius, *M. alterum pannonicum*, or is it *AL incanum*, or a muddle of both? Linnaeus has certainly mixed up these under (a) and possibly *AL paniculatum* Desr. and *Af. praeceox* Janka as well. This is the justification for preferring (8) as entitled to the specific name in this case. Of the two synonyms quoted, that of Clusius is the really important one. *M. album latifolium peregrinum* C. B. P. is not a little confused, as has been pointed out by Kerner t, and may be seen b\ reference to the conflicting older names quoted for it by Bauhin himself, Pin. p. 230. Morison's figure, Hist. iii. s. 11, tab. 9, fig. 8, cited by Linnaeus in support of it, evidently represents the same plant as that of Clusius t, who in liar. Stirp. Punn.

\* Of course no weight attaches to Miller's geography ; the countries of origin in the Gardener's Dictionary are frequently unreliable. I have previously had occasion to point this out in Nuov. Giorn. Bot. It. xxv. p. 39 in respect of *Bianthus ferruyinew*. Another obvious case is *Pulmonaria saccharata*; but in the genus *Marrubium* Miller excels himself. For his no. 3, *creticum*, he assigns Spain and Portugal; no. 5, Spanish ~~if~~ *supinum*, he banishes to the islands of the Archipelago; no. 0, the certainly Oriental *candidissimum* etc. of Hort. Cliff., flies west to Spain, an impossible habitat even if *M. incanum* were intended.

f Kerner's important discussion of *M. peregrinum* and *M. remotum* in Oestr. Bot. Zeit. xxix. (1874) pp. 339-34:?, is referred to.

X In the separate detail the calyx seems to show more than five teeth, but this is probably bad drawing, as it is shown with five on the plate, and in the text, p. 377, Morison says "calycibus quinquefariam in margine divisus."

(1583) had described and figured, as *Marrubium alterum pannonicum*, a species which he declares to be very common in Austria and Pannonia. "Adeo vulgare est in toto Viennensi agro, ut vinetorum agrorunique marlines, sicque et graminei campi eo abundant." It would seem to be on this figure of Clusius that; 0. Bauhin based his *M. album latifolium peregrinum*, and it is regarded by Jacquin as being the very plant depicted in his tab. 160. Now it is certain that the plant of Clusius's woodcut is not *incanum*, though it differs somewhat in leaf-outline from Jacquin's. Was it nothing but a broader form of the common Viennese plant? ; in which case the difference between *latifolium* and *angustifolium* would shrink to one too slight for Linnaeus to have subdivided his species on that ground alone. Quite another view is taken by such eminent botanists as the elder Reichenbach, Koch, Bentham, and Boissier, who all refer Clusius's name and figure to a different species, usually known as *M. remotum* Kit. (in Schult. Oesterr. Flora, ed. 2, ii. p. 161, 1814), but of which *M. paniculatum* Desr. (in Diet. Encyc. iii. p. 716, 1789) is the earliest name.

Kerner has completely demolished this theory. Although *M. paniculatum* grows in Austria as well as in Hungary, it is exceedingly rare near Vienna, where it occurs only occasionally in the company of *M. peregrinum* and *M. vulgare*, between which it has been considered by most Austrian botanists to be a hybrid. It cannot be supposed that Clusius was speaking of so rare a plant when he said, "*vulgare est in toto Viennensi agro.*" It is the figure—the figure only and no words of Clusius—that led Reichenbach, Koch, and the rest to identify *M. alterum pannonicum*, and consequently *M. peregrinum* (B) with *M. paniculatum*. The figure indeed has more likeness, owing to the broader leaves, with rather sharper serratures and the longer bracts, to Reichenbach's plate of *paniculatum* in Ic. Crit. iii. fig. 473 than that of *creticum*, *ibid.* fig. 461. But Clusius has distinctly shown the calyces with five teeth, as they constantly are in *creticum*, whereas in *paniculatum* they are irregular in number, between 5 and 10. The conclusion is that Clusius meant the very same plant as Jacquin, in spite of the broader leaves of the figure. As Kerner points out, the earlier leaves of *peregrinum* are always broader than the later, so that the appearance of a specimen depends much on the stage at which it is gathered, and in those from hotter or drier countries the broad leaves fall away sooner than in milder climates. We must therefore reject the synonymy given by Koch in all editions of the Synopsis before the last. "*M. peregrinum* L. occurrit (a) *latifolium* <sup>^</sup>*M. peregrinum* W. = *M. paniculatum* Desr. = *M. remotum* Kit.; (b) *angustifolium* = *M. peregrinum* Jacq. = *M. creticum* Mill." In the last edition Brand alters this by confining the name *peregrinum* to (f) and transferring (c) to a separate hybrid species.

But merely to unite (a) and (f) as insignificant forms of one species, as in

Rchedse ad Fl. Exsicc. Austr. Hung. no. 171, is too ingenuous. The case is not so simple as that. When the Linnean specimens are examined they show among other things that Linnaeus included under *peregrinum* (a) not only the plant of Clusius but also *incanum*, being apparently unconscious of the contradiction. Thus in Herb. Hort. Cliff, the specimen of *album angustifolium peregrinum* is precisely Jacquin's plant, but *album latifolium peregrinum* is represented by an example of *incanum*. In Linnaeus's own herbarium we find for *peregrinum* (without distinction of (a) and (f)) the sheet no. 15 already mentioned, containing both *incanum* and *supinum* but no true *peregrinum* (*creticum*), on which the label has been altered from *peregrinum* to *candidissimum*. This sheet then, before the alteration of the label, so far agreed with the Hort. Cliff, specimen and with Linnaeus's note to Hort. Elth. fio\*. 21 f. as to indicate *incanum* as being *peregrinum* (a). Of course one would like to say on the strength of these specimens and of the note, "Koch as well as Kerner are all wrong; *peregrinum* (a) is neither *remotum* nor Jacquin's *peregrinum* but *incanum*, which would otherwise be entirely omitted by Linnaeus, an untenable supposition, since it exists in both herbaria and, as already explained, cannot be *candidissimum*." But then we should contradict the only reliable synonym, that of Clusius, and also that of Morison and to a great extent that of Bauhin also. The only possible conclusion is to drop the use of the Linnean name for the plants confused under (a) and restrict it to the well-defined (13) with narrower or wider leaves. We may safely do this in spite of the hitherto unnoticed incompatibility of yet another specimen. As already mentioned, the Hort. Cliff, example of (f) is Jacquin's species, but the corresponding one in Herb. Linn., now bearing the number 2, is something else. It is named by Linnaeus "*peregrinum* (f)" with "*M. album angustifolium* C. B." written on the back, and is marked f, showing that he had received it from Gerber, who travelled in south-eastern Russia. It is also labelled in another hand—perhaps Gerber's own—" *Manbium album angustifolium ad fluv. Axey*." This is an old spelling of Ak-sai, the name of two rivers Yesaulovskoi Aksai and Kurmoyarski Aksai, which rise in the western hills of Astrachan and flow westward into the Don. The usual maps and gazetteers will show the town Aksni even if the rivers are not marked. There are in the possession of the Linnean Society two MS. lists of plants collected by Gerber. No. 1, Flora Wolgensis, under no. 1064 names *M. album angustifolium peregrinum* as growing "in desertis Donnensibus inter Glasunowski et Saratowa"; no. 2, Floni Tanaensis, which is in the handwriting of Linnaeus himself, contains, no. 1522 "*M. album angustifolium, ad fl. Axey*." The specimen itself is a good example of *M. pumila* Janka, in Oestr. Bot. Zeit. xxv. (1875) p. 62, a species which extends from Transylvania eastward and seems to be plentiful in southern Russia, though often unrecognised. I have myself an example collected by Zehner at Neidlich on

the sea of Azov in 1869, which is identical with that of Linnaeus \*. In habit *M. prcecox* resembles *M. paniculatum* more closely than *M. creticum*, and has been mixed up with it by Boissier in Fl. Or, iv. p. 792. They are often confused and wrongly labelled in herbaria. Here are Janka's distinctions : "*M. peregrinum*" (*creticum*); "calycis tubus obconico-campanulatus; dentes semper 5 triangul-acuti, crassi, recti; basi sinu acuto confluentes. *M. prcecox*; calycis tubus cylindricus ; dentes semper 5 subulato-setacei tennes recti; basi interstitio sejuncti." I may add that in *prcecox* the bracts are a good deal longer than in *creticum*^ though not so long as in *incanum*, and the serratures reach nearly to the base of the leaf. *M. paniculatum* is, of course, distinguished by its larger number of calyx-teeth. The superficial resemblance of the Linnean specimen of *prcecox* to *creticum* is quite close enough to account for its having been unsuspectingly passed as *peregrinum* ; it need not disturb our acceptance of *creticum*, Jacquin's plant, as being the true and only heir to the Linnean title *peregrinum*.

One word as to the *habitat* assigned by Linnaeus for *M. peregrinum*. In Hort. Cliff, he says, "circa Messanam Sicilise, in Creta et in agro Viennensi" ; in Sp. Pl. "in Sicilise, Cretse, Austria siccis" and in ed. 2 he adds "in Libano" for *peregrinum* (*ft*). Crete and Vienna have already been discussed ; in the absence of a specimen it is impossible to say what the reference to Lebanon means ; the only species mentioned in Fl. Or. for those mountains being *M. cuneatum* and *M. libanoticum*, neither of which resemble *peregrinum*.

The Italian floras, e.g. Fl. Anal, d'Italia, iii. p. 20, are not aware of the presence of either *incanum* (their *candidissimum*) or *peregrinum* in Sicily. I was therefore surprised to find in Herb. Gay at Kew a specimen of *incanum* sent from that island by Jan as *M. candidissimum* Linn, and included in his \*Elenchus' of 1827, p. 9, as well as another in Herb. Mus. Brit. received from Gandoger with the label "*Marrubium candidissimum* in Sicilia prope Caltanissetta legit Reimbole, Septr. 1872." It therefore seems probable that the *M. supinum* quoted by Ucria, Hort. Pan. p. 248, for Sciacca on the south coast of the island is *incanum*. The presence of *peregrinum* in Algeria is uncertain ; cf. Battandier, Fl. Alg. p. 695.

\* For *M. prcecox* I rely also on (1) J. Barth, anno 1895, from Alárog-Hudoz ii Transylvania; (2) Sintenis, anno 1873 no. 275, from Babadagh in the Dobrud<jcha (as *M. remotum*) ; (3) Nordmann in herb. Bentham, from Odessa (as *M. peregrinum*); (4) Callier, It. taur. secund. 1896 no. 180, from Burunduk in the Crimea; (5) Plerb. Flor. Rossi@ no. 835, "in steppis prope urbem Taganrog." This is near Gerber's locality. The label includes an obs. by D. Litwinow: "*M peregrinum* L. in Caucaso videtur vulgatissimum septentrionem versus, in steppo Rossise meridionalis valde rarescit."<sup>1</sup>

## III.

## MARRUBIUM PANICULATUM.

The discussion of *M. peregrinum* has called our attention to *M. paniculatum* Desr., in Diet. Encyc. iii. p. 716 (1789). This species is more usually known as *M. remotum* Kit. in consequence of a doubt as to the identity of *paniculatum* expressed by Bentham, Lab. p. 590, under *M. pannonicum*, for which I see no sufficient reason, although the synonyms quoted are rather mixed and the chief characteristic—the number of calyx-teeth—is not mentioned. Herb. Lamarck contains a specimen agreeing with *remotum*, originally labelled *paniculatum* although the label has been subsequently altered to *peregrinum*, which it is not. *Peregrinum creticum* appears both in Diet. Encyc. and in Herb. Lamarck under the latter name. Herb. Tournefort contains two sheets, 1287 and 1288, referable to *paniculatum*, although labelled *M. album angustifolium peregrinum*, of which there is no true example in that herbarium. Reichenbach adopted Desrousseaux's name in Ic. Grit., although he thought it "*nomen ineptum*," but for that reason he altered it in Fl. Germ. Exc. p. 325 (1830) to *M. pannonicum*, regardless of the existence of the earlier *M. remotum* Kit. of 1814.

Most Austrian botanists have adopted the view of Reichardt, in the Vienna zool.-bot. Verhandl. xi. p. 342 (1864), that *paniculatum* is nothing more than a bastard between *vulgare* and *peregrinum*. This suggestion must have been put forward at a much earlier date, though ignored by Kitaibel, Koch, and the Reichenbachs, because it is criticised by Bentham, Lab. p. 591, on the ground that "natural hybrids appear scarcely possible in a genus where, like *Marrubium*, the stamina and style are enclosed in the tube of the corolla." Such an objection can hardly be sustained. There lies before me a very evident hybrid between *supinum* and *vulgare* collected by Pau near Segorbe in Spain. There is, however, another side to the question. Kerner, *loc. cit.*, points out that although in Germany, where it is found at Erdeborn near Halle, and in Austria, this is a rare plant only seen where its presumed parents grow; it is widespread in Hungary, very plentiful where it occurs, often present where there is no *vulgare*, outnumbering *peregrinum* where they grow together, here and there covering whole stretches of country and spreading itself successfully by seed.

All that is very unlike the behaviour of an ordinary bastard. I must confess that in the specimens I have seen I can discover little or no evidence of hybridity with *vulgare*. The calyx-teeth, although more numerous than in *peregrinum*, have no resemblance to those of *vulgare*, nor have the leaves. If it were not for the opinion of those who know the plant in its natural surroundings, I should refuse to admit its hybridity on herbarium evidence alone. Some further details may be found in a paper by Borbas, "*Zur Flora von Mittel-Ungarn*," in the same vol. xxiv. of Oestr. Bot. Zeit. p. 343. These do not seem to be quite in accord with Kerner's assertions. Kern<sup>r</sup>

suggests, however, that the plant is an instance of the establishment of an independent species from originally hybrid individuals, and adduces it in his paper "Können aus Bastarten Arten werden?" in Oestr. Bot. Zeit. xxi. (1871). Is it not possible that all the individuals found in the western part of the area, where *paniculatum* fails to spread itself, and also some of those in Hungary, may be hybrids in the ordinary sense, while more favourable conditions in other districts have led to its establishment independently of the parents? A final explanation must rest with Hungarian botanists who can follow up the different forms in the field. It must not be forgotten that at the date of Kerner's paper Janka's *M. preeceox* had not yet been distinguished. Though referred to without being named in Borbas's paper, it was not published till the following year, 1875.

#### IV.

##### MARRUBIUM SUPINUM.

This Spanish species, which extends to Algeria, affords another instance of the greater reliability of specimens in Herb. Hort. Cliff, than of those in Herb Linn, in this genus. *M. supinum* of Sp. PL is identical with no. 6 in Hort. Cliff., defined as *At. denticulis calycinis rectis villosis*, with references to *M. album sericeo parvo et rotundo folio* Barr. Ic. 685 and *M. hispanicum majus* Barr. Ic. 686, as well as to *M. hispanicum supinum foliis sericeis argeateis* Tourn., and to Hispania as habitat. It is represented in the Hort. Cliff, herbarium by a specimen labelled with the Tournefort name, though *sericeis* is misspelt *cerisiis*, and in herb. Tournefort by no. 1289. Both are the Spanish plant usually and rightly called *M. supinum* Linn. In Sp. PL. Linnaeus repeats for his no. 4 *supinum* what had been said in Hort. Cliff., with the omission of the Tournefort synonym and the addition of Gallia Narbonensis to the habitat.

There cannot be the slightest doubt about the identity of the species, though it was misunderstood by Scopoli, who took *M. incanum* for it, leading to the erroneous addition of Carniola to the habitat in Willd. Sp. PL. iii. p. 111. It is strange that Bentham, Lab. p. 742, should not have known the plant and suspected Linnaeus to have been describing a garden hybrid. He cannot have looked at the Hort. Cliff, specimen. This mistake he corrected in DC. Prodr. xii. p. 450, but meanwhile it had led Boissier, Voy. ii. p. 509, to substitute the name *sericeum* for *supinum*. Boissier also hesitated on account of the inclusion in the habitat of Gallia Narbonensis, where the species does not grow, and of the citation of Barr. Ic. 686, which he thought "s'applique a une espèce toute différente," without saying to what species. Those suspicions are quite unfounded. Gallia Narbonensis is obviously a mistake, and Barr. 686 really resembles Boissier's own figure cxlviii. more closely than does Barr. 685. Indeed Rouy, Exc. Bot. en 1881 et 1882, p. 80 (1883), in distinguishing three varieties of *supinum* quotes Barr. 686 for his var. *Boissieri* and 685 for his var. *Barrelieri*.

The only trouble (of which Boissier was unaware) is about sheet no. 8 Herb. Linn, which is labelled "*supinum* 7." It is an old Hort. Cliff, sheet with the flower-pot design, but *supinum* must be a slip of the pen, for the specimen is not *supinum* and that name does not correspond to no. 7, which both in Hort. Cliff, and in Herb. Sp. Pl. is *M. hispanicum* Linn. The specimen, which is *sine loco*, will not do either for no. 7 or for *supinum*, being in fact the Italian and Dalmatian *Ballota rupestris* Vis.=i?. *italica* Benth., and is referred to in Bentham's footnote to *B. italica* in DC Prodr. xii. p. 519. This unfortunate specimen no doubt played its part in Bentham's earlier confusion of his eastern *B. italica* with his western *B. hirsuta*. There is only one scrap of true *supinum* in Herb. Linn. It lies unrecognised on sheet no. 3 alongside of a good example of *M. incanum*, which has been mentioned in my note on *M. candidissimum*.

## V.

### MARRUBIUM HISPANICUM—BALLOTA HISPANICA—BALLOTA HIRSUTA.

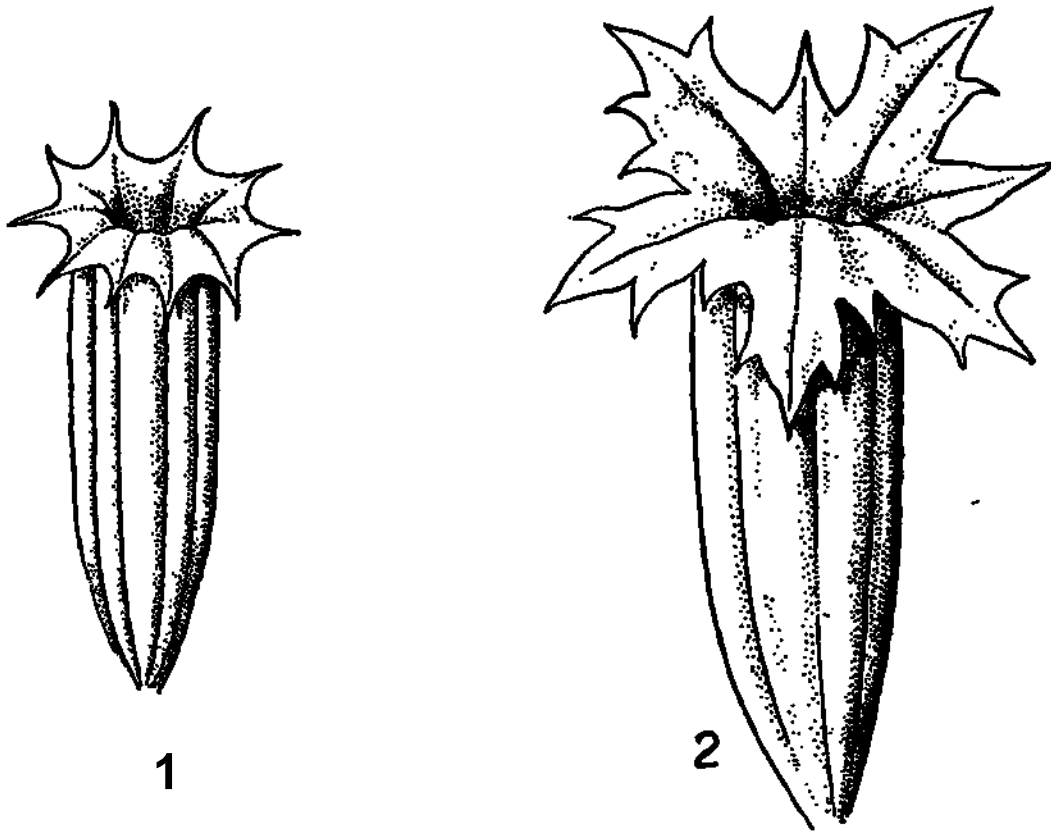
*Marrubium hispanicum*, placed by Linnæus among those "calycibus 10-dentatis," and subsequently transferred to the genus *Ballota*, will involve us in a tiresome discussion of the nomenclature of two very different plants, a Spanish and North African species usually known as *Ballota hirsuta* Benth., and another that inhabits both sides of the Adriatic, commonly called *Ballota rupestris* Vis. The accompanying figure displays the striking difference in their calyces. The conclusion will be that all the current names must be abandoned ; that Linnæus's name belongs exclusively to the Spanish species, for which it must therefore be retained as *Ballota hispanica* (Linn.) nobis, non Benth., while the Italian plant should be called *Ballota hirsuta* (Willd.) Kerner, non Benth.

The Linnean name has been the subject of almost incredible confusion between the Spanish species, which does not extend to the central and eastern Mediterranean, and the Adriatic or Italian one that does not grow in Spain. That *Marrubium hispanicum* of the Sp. Pl. really is the Spanish kind, is conclusively proved by: (1) the diagnosis and observation, "calycum limbis patentibus, denticulus acutis . . . . calycis limbo glabro, angulis 10 acutis," which are inapplicable to the Italian plant; (2) the reference to Hort. Ups. p. 169, where it is said that compared with *M. Pseudo-Dictamnus* "calyx in hac magis stellatus et plicatus dentibus acutis," a remark that would not be true of the Italian kind; (3) the quotation of *M. subrotundo folio* Barr. and bis Ic. 767 ; (4) the twice repeated "habitat in Hispania"; (5) the unmistakable specimen of the Spanish species from Hort. Ups. on sheet no. 9 in Herb. Linn., labelled "*hispanicum*" by Linnæus himself.

The only possible objections are : (a) the quotation of Herm. Par. tab. 201 (1705), a figure which, although referred by some authors to the Spanish species, to my eye represents very clearly the Italian one. This is borne out

by the language in which Hermann differentiates his *M. album rotundifolium Hispanicum maximum* Schol. Bot. Par., of course a garden plant, from *Ocy-mastrum Valentinum* Clus. This quotation, however, only amounts to the insertion by Linnaeus of one mistaken synonym in his otherwise perfectly consistent account of the Spanish *Marrubium hispanicum*. (b) The presence of four Hort. Cliff, specimens—three of them in Herb. Hort. Cliff, and the fourth in Herb. Linn, sheet no. 8,—which are the Italian species. Now, although at the beginning of this series of *Marrubium* notes I have pointed out the greater importance of Hort. Cliff, specimens in the genus, this instance forms an

FIGS. 1 &amp; 2.



1. *Marrubium hirsutum* Willd.  
*Ballota hizpanic\**. Benth.; *B. italica* Benth.  
The Italian species, enlarged about X 7.

2. *Marrubium hispanicum* Linn.  
*Ballota hirsuta* Benth.  
The Spanish species, enlarged about X 8.

exception. They cannot prevail where they are in such flat contradiction with diagnosis and habitat, while the Linnean specimen, sheet no. 9, agrees. The peculiarity of sheet no. 8 has already been explained under *Marrubium supinum*.

The Spanish plant first appears in Clusius, Bar. Stirp. Hisp. p. 392 (1576), where it is well figured under the name of *Qcymastron Valentinum*; Barrelier afterwards pictured it as *Marrubium hisp. rotumlifol. album majus seu latifoliu.* fig. 767, copied as usual by Boccone, Mus. tab. 122. Brotero, Phytogr. tab. 110, and Hoffmg. & Link, tab. 8 show admirable figures of *Marrubium cinereum* Dear., which is so closely allied as to be treated by Willkomm in



Prodr. Fl. Hisp. ii. p. 446 as identical, and by Bentham, Lab. p. 596, and Rouy, Scrinia fasc. xi. p. 259, as var. *hispida* Benth., though kept up as a species by Coutinho, Fl. Port. p. 251, as *B. cinerea* Briq.

The name *Alarrubium hispanicum* has been correctly applied by Willdenow, Sp. Pl. iii. p. 113 (1800), by Desfontaines, Fl. Atl. ii. p. 23, also of 1800\*. On the other hand it has been misapplied to the Italian species by Petagna, List. iii. p. 816 (1787), by Sprengel, Syst. Veg. ii. p. 740 (1825), by Gussone, Fl. Sic. Prodr. ii. p. 106 (1828), by Tenore, Syll. p. 292 (1831), and by Host, Fl. Anstr. ii. p. 173, in the same year (1831), and notoriously by Bentham, loc. cit. (1834), where after a good description of the Italian plant, Spain is erroneously included with Sicily, Italy, and Dalmatia in the *habitat*, while the Spanish plant is also well described, but under the name of *Ballota hirsuta*, on the false assumption—though marked with a query—that it is the *Marrubium hirsutum* of Willdenow, Sp. Pl. iii. p. 113. Some time, however, after the publication of the Lab. Gen. et Spec. Bentham visited Berlin, and discovered that *Al. hirsutum* of Herb. Willdenow, no. 10923, is not the Spanish but the Italian kind. See his "Herb. Willd. Didynam. Gymnosperm. cum inonogr. Beuth. comparatum" in Linnæus, xi. p. 601 (1837). The consequence of this discovery and of the remarks of Gussone in Fl. Sic. Syn. ii. p. 83 (1843; was that in DC. Prodr. xii. (1848) Bentham altered the name of his *Ballota hispanica* to *Ballota italica*, cutting out Sp. from the *habitat*. His new and most appropriate name came too late, for in the preceding year Vavani had already transferred Bivona's *Marrubium rupestre* of 1814 to the genus *Ballota*. Unfortunately Bentham failed to complete his correction by abandoning his name *B. hirsuta* for the Spanish plant, and transferring to it the name *B. hispanica*, as he had better have done.

It must accordingly be taken as established that Willdenow's *hirsutum*, although he did not know its origin, is the Italian plant. This, as pointed out by Visiani, loc. cit., is obvious from the distinctions he draws between *Al. hirsutum* "calycum dentibus patentibus lanceolatis," and *Al. hispanicum* "calycum limbis patentibus, dentibus ovatis imicronatis," which admirably expresses the distinction so clearly shown in the figures herewith, it is confirmed by Bentham's inspection of the herbarium specimen. The conclusion is therefore irresistible that the name *Ballota hirsuta* must be abandoned for the Spanish plant, and adopted for the Italian species in preference to *B. saxatilis* based on *Marrubium saxatile* Raf. (1814), and to *B. rupestris* based on *M. rupestre* Biv. of the same year, but later, because Bivona quotes Rahn's name, or to *B. italica* Benth.

It remains to inquire how so great a botanist as Bentham could have fallen into the two errors of (1) supposing that Linnæus's name *hispanicum* and its diagnosis belonged to the Italian species, and (2) fancying that the Italian

\* *M. hispanicum* Dear, in Diet. Enoyc. iii. p. 719 (1789; is rather ambiguous, but the description of the calyx seems drawn from the Italian plant as grown at Paris.

species grew in Spain also. There were, in fact, several traps laid for him. As to (1), there was the presence of no less than three Hort. Cliff. specimens—though not actually referred to by Bentham—labelled respectively (a) "*Pseudodictamnus Hispanicus foliis amplissimis, ügricantibus et villosis*," (b) "*Pseudodictamnus Scrophularice folio*," and (c) "*Pseudodictamnus Hispanicus amplissimo folio candicante et villoso*," all of which are Tournefort synonyms quoted in Hort. Cliff., but omitted in Sp. PL, for *Marrubium calycum litnibus patentibus, denticulis acutis*. It is of no concern to us whether the Tournefort synonyms were rightly affixed to these, or not; the important point is that all three are the Italian (or Dalmatian) species. There is no example of the Spanish *hispanicum* in Herb. Hort. Cliff. Then there is the other sheet in Herb. Linn. no. 8, already described under *M. supinum*, which, although so labelled, carries a specimen identical with the last-mentioned three of Hort. Cliff., whence it came. This is referred to by Bentham in DC. Prodr. xii. p. 519 in his note to *B. italica*. Moreover, in Herb. Banks he had seen a Chelsea-garden specimen, no. 2680 of the year 1774, labelled *M. hispanicum*, which is obviously the Italian kind.

As to (2), his unfortunate quotation of Hispania among the habitats of *B. italica* no doubt was due to the presence in Herb. Banks of another sheet of undoubted "*italica*," labelled *Af. hispanicum* and *a tergo*, "Spain, ex herb. Pavon." Now it may be that the specimens came from Herb. Pavon, but it never grew in Spain, where the species has never been seen in later times, and where it is against all geographical probability that it should occur. Thus Bentham's error, if not justified, is at any rate explained.

It is unlucky that Bentham's misuse of the name *Ballota a hispanica* should have been an obstacle hitherto to its correct employment for the Spanish species. The following chronological synonymy avoids disturbing *B. saxatilis* Sieber ex Benth. (1834), which might have to give way if Willdenow's name is not accepted for the Italian plant, for which *M. saxatile* Raf. is the next earlier specific.

*For the Spanish species.*

BALLOTA HISPANICA nobis, 1925.  
*Marrubium hispanicum* Linn. 1753.  
*Berlinyera hispanica* Neck. 1790.  
*Marrubium hispanicum* Willd. 1800.  
 " " Deaf. 1800.  
 " *tinereum* p. pte., Spreng, 182-3.  
*Ballota Ursula* Benth. 1834.

*For the Italian species.*

BALLOTA HIRSUTA Kerner, 1884.  
*Marrubium hirsutum* Willd. 1800.  
 " *saxatile* Raf. 1814.  
 " *rupestre* Biv. 1814 (later).  
 " *hispanicum* Spreng. 1825.  
 " " Guss. 1820.  
 " *hirsutum* Keichb. 1880.  
 " *hispanicum* Ten. 1831.  
 " " Host, 1831.  
*Ballota hispanica* Benth. 1834.  
 " *saxatilis* Guss. 1842.  
 " *rupestris* Vis. 1847.  
 " *italica* Benth. 1848.  
*Berlinjera hirsuta* Nym. 1854.  
*Ballota hirsuta* Halácsy, 1902.

If it should be thought that Kerner's *Ballota hirsuta* is inadmissible owing to his mistaken quotation of *B. hirsuta* Benth. as identical, the name would still prevail, but be attributed to Halácsy, as above.

If *Berlingera* were to be kept up as a genus, all the trouble would be avoided. We should have *Berlingera hispanica* Neck. (1790) and *Berlingera hirsuta* Nym. (1854).

## VI.

### MARRUBIUM CIRCINNATUM.

*Marrubium circinnatum* Desr. in Diet. Encyc. iii. p. 217 (1789) was described from a single specimen in Herb. Jussieu. Ben than), in Lab. p. 592 and in DC. Prodr. xii. p. 454, treats this species as "non satis notaj" merely transcribing Desrousseaux's description. Boissier, in Fl. Or. iv. p. 702, more rashly identifies it with *M. velutinum* Sibth. et Sin. Evidently neither of them had inspected the type which still lies in Herb. Jussieu at the Paris Museum, under no. 5578, labelled "*Marrubium album foliis amplis fere circinnatis*," without any indication of origin. It is obvious at a glance that the plant is not *M. velutinum* but *M. rotundifolium* Boiss., Diagn. ser. 1, 5, p. 33 (1844). The characters by which *rotundifolium* is distinguished from *velutinum* by Boissier, *loc. cit.*, and in Fl. Or. iv. p. 698, are conspicuous in Jussieu's specimen, which agrees with those collected on Mount Sipylus in Lydia by Balansa, Pl. d'Orient, 1854, no. 329, and by Bornmüller in 1906, no. 9905, as well as on M. Tmolus above Philadelphia by Boissier himself. Herb. Banks in Mus. Brit, contains a specimen labelled "*Marrubium folio subrotundo* Bocc, a D. Sherard 1719" which is identical with the plant in Herb. Juss., and of course should not bear Boccone's name, which belongs to *M. supinum* Linn.

Tournefort is very likely to have met with *M. circinnatum* on M. Sipylus on the 17th December, 1701 : "nous nous amusâmes ce jour là à herboriser sur le Mont Sipylus" (Voyage, ii. p. 492). This record induces me to think that *M. album incanum candidissimum et villosum* was very possibly *M. circinnatum*. Though it would not have been in flower in December, which might account for the absence of a specimen in Herb. Tourn., he may have brought home plants which afterwards furnished the specimens of Jussieu and of Bherard.

## VII.

### MARRUBIUM in Herb. Tournefort.

The seven species of *Marrubium* enumerated in the 'Institutions/ pp. 192, 193, are European ; the remaining four, which are Oriental, are mentioned in the 'Corollarium,' p. 12. It may some day be of use to a monographer of the genus to record which of these are represented in Tournefort's herbarium at the Paris Museum.

1. *A*, *album mdgare* C. B. P. is represented in the herbarium by sheet no. 1284, which bears no label.

2. *M. album villosum* C. B. P., so labelled on sheet 1283, is the form of *vulgare* that corresponds to *M. apulum* Ten.

3. *M. album latifolium peregrinum* (J. B. P., so labelled on sheet 1285, is *M. incanum* Desr. = *M. candidissimum* auct. non Linn.

4. *M. album peregrinum, brevibus et obtusis foliis* C. B. P., with syn. *M. creticum angustis foliis inodorum* Eyst., is not represented in the herbarium.

5. *M. album angustifolium* O. B. P., with syns. *M. album angustiore folio* J. B. and *M. creticum* Tab., is represented by two identical specimens, nos. 1287 and 1288. These have broadish leaves, a large spreading panicle, and more than 5 calyx-teeth. They are *M. paniculatum* Desr. = *M. remotum* Kit.; they do not therefore seem to agree with the name.

6. *M. hispanicum supinum calyce stellato et aculeato* with syn. *Alyssum Galeni* Olus. is obviously represented by sheet 1286, though unlabelled. The specimen is *M. Alysson* Linn.

7. *M. hispanicum supinum, foliis sericeis argenteis* with syn. *M. album sericeo parvo et rotundo folio* Bocc. is represented by sheet 1289, labelled *Marrubium d'Espagne* and *Marrubium hispanicum sericeum incanum* Alt/sso *Clusii congener; Jlore purpurascete*. It is *M. supinum* Linn.

8. *M. album candidissimum et villosum*. This is undoubtedly the name for an Oriental species, like other names in the \*Corollarium.' It is unidentifiable, because not really represented in the herbarium, although on the label to sheet 1290 we read *Marrubium album grsecum foliis ad basin acutis*; *M. album candidissimum et villosum* (JoroJl. Inst. But both this no. 1290 and the similar unlabelled 1291 are just forms of *M. vulgare*, with upper stem-leaves not cordate or rounded at the base but tapering into the petiole. They both have the characteristic ten-hooked calyx-teeth of *vulgare*. The label may have been accidentally attached to a wrong sheet, or, if Tournefort meant to call these specimens *M. album gracum foliis ad basin acutis*, which is not improbable, the synonym *M. album candidissimum et villosum* has been added by an oversight of his own or of some other person who wrote the label.

9. *M. Orientale, foliis subrotundis, Jlore purpureo. Idem Jlore albido*. Sheet 1292, labelled *M. cappadocicum, foliis subrotundis Jlore purpureo*, corresponds to this and is *M. astracanicum* Jacq., as has long been recognised. No. 1293 bears a similar label with *Jlore albo* instead of *Jlore purpureo*. There is another Tournefort specimen of each of these in Herb. Banks at the British Museum; they were used by Bentham for his description of *M. astracanicum*. In Herb. Jussieu there lies a pretty woodcut, *ic. ined.*, of one of these or of a similar specimen with the legend *M. orientale foliis subrotundis (&ic) Jlore purpureo*.

10. *M. Orientale angustissimo Jolio Jlore albo* is not represented in the herbarium.

11. *M. Orientate, Catariw folio, flore albo* represented by sheet 1294, which is labelled *M. ibericum, Catariw folio, flore albo*, is *M. catarurfoliuni* Desr., as pointed out by Boissier in Fl. Or. iv. p. 700. There is another Tournefort example of this in Herb. Banks.

It will be noticed that species 4 and 10 are not found in the herbarium, that the specimen for no. 5 does not exactly correspond to the name, "M<sup>d</sup>" that for no. 8 not at all.

### EXPLANATION OF THE PLATES.

#### PLATE 2.

*Marrubium folio candidissimo orbiculare, crassissima*, from the Cliffordian Herbarium, in the British Museum (Natural History).

#### PLATE 3.

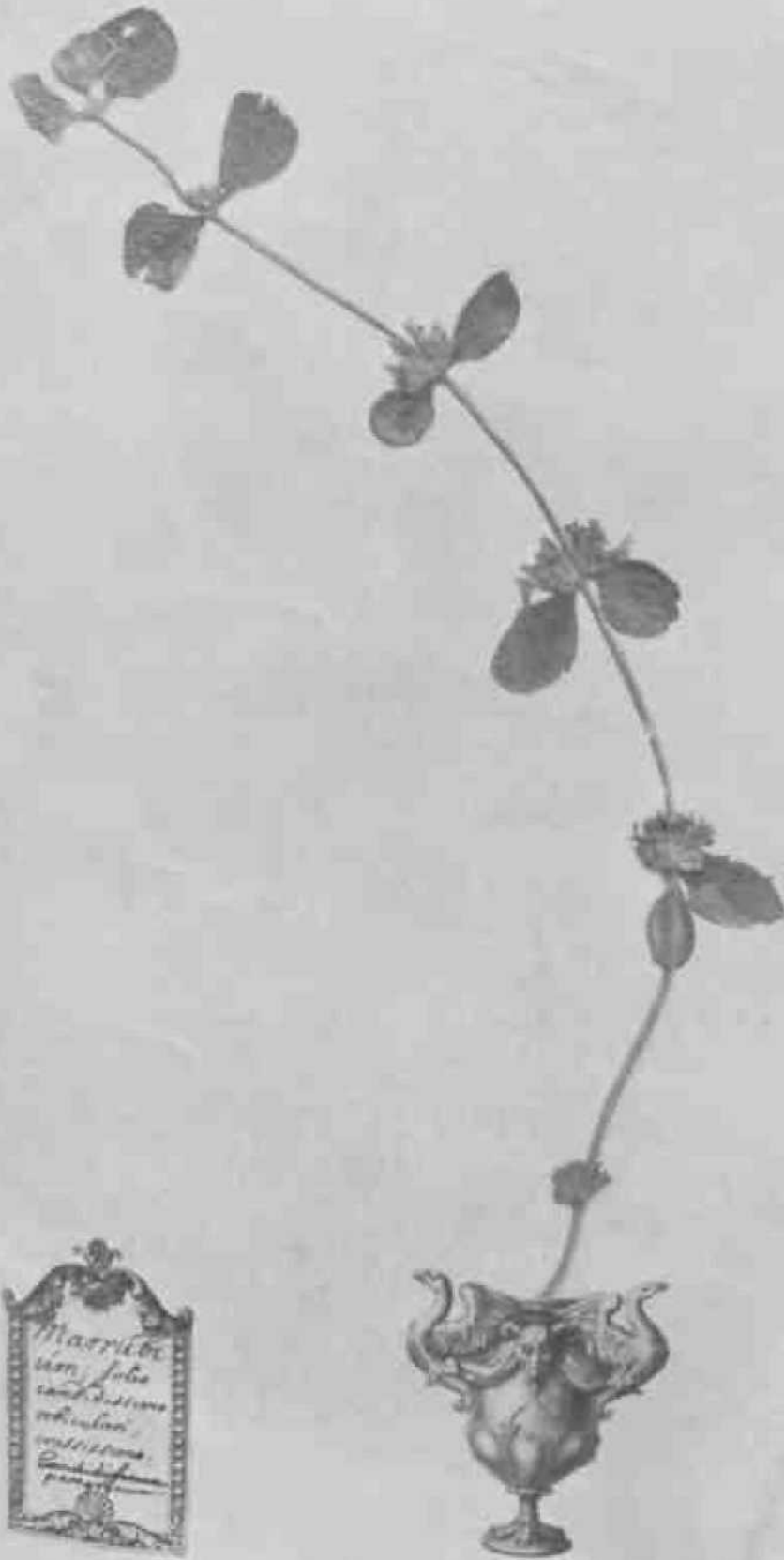
*Marrubium folio rotundo candidissimo*, from the Cliffordian Herbarium.

### COLCHICUM MONTANUM.

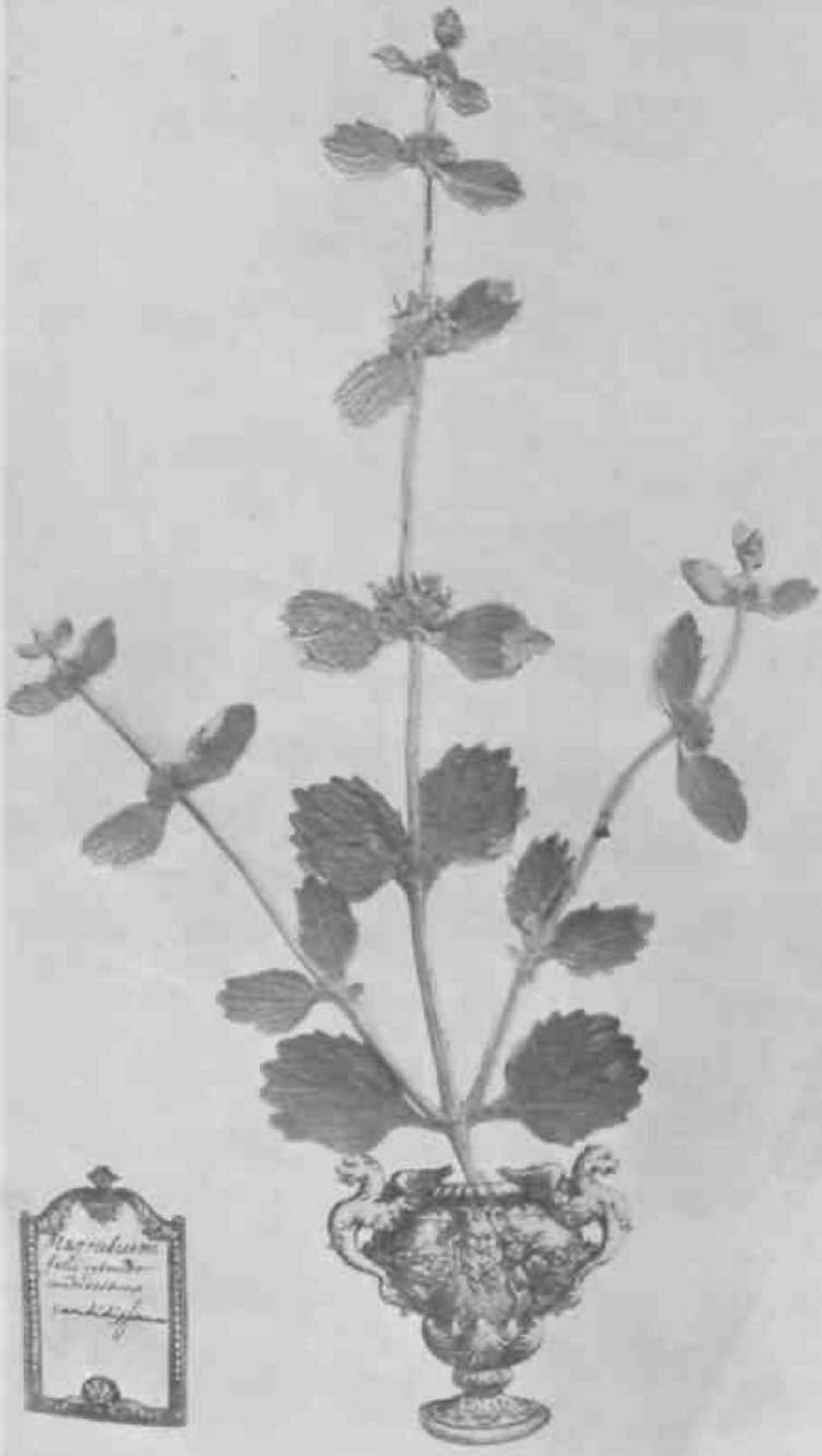
This is a name that must be abandoned. It is a striking instance of the confusions that abound in 'Species Plantarum' where *C. montanum* is a mixture of *Merendera Bulbocodium* Rum. from the Pyrenees and Spain with *Colchicum alpinum* DC. from the Alps and northern Apennines. Neither bears any resemblance to *Colchicum Bertolonii* Stev., the common synanthous-leaved *Colchicum* of Italy, to which name *C. montanum* Linn, has so often been wrongly applied.

Linnaeus does not himself describe *C. montanum*, but merely quotes Loeffling's diagnosis, "*Colchicum foliis linearibus patentissimis*," and two synonyms, *C. montanum angustifolium* Bauh. Pin. and *C. montanum* Clus., with Hispania et Helvetia as habitat. Now the plant described and figured by Olusius, Rar. Stirp. Hisp. p. 266, was found by him on the stony hills near Salamanca, where he says it was called *Merenderas* or *Quitameriendas*. This is notoriously *Merendera Bulbocodium* Ram. = *Merendera montana* Lange, and is the very same plant that Loeffling saw plentifully in the plains of Estremadura and Oastile on his journey from Lisbon to Madrid in October 1751, though he did not attempt to distinguish it generically from *Colchicum*. See his letter to Linnaeus of Nov. 1, 1751, in his Reise, p. 26. All this was indicated long ago by Lapeyrouse, Hist. Pyr. p. 201 (1813), and has been accepted by Willkomm & Lange and by Parlatores. Then the Bauhin synonym, which accounts for the "habitat in Helvetia," is admittedly *C. alpinum* DC., Fl. Fr. iii. p. 195 (1805), where—by the way—the name *C. montanum* is misused.

We cannot adopt the name *C. montanum* Linn, for Clusius and Loeffling's Spanish plant, except by transferring it to the genus *Merendera*, as Laiige has done, to replace *Merendera Bulbocodium*. On the other hand we must



IWARRUBIUM GLOBOSUM No. 1.



*Marrubium  
glaberrimum  
L.*



MARRUBIUM GLABERRIMUM N° 2.

not say « *C. montanum* Linn, is *C. alpinum* DC," because the diagnosis, such as it is, was intended by Loeffling for the Spanish *Merendera* and not for any *Colchicum*. Nor can we say that *C. montanum* is the plant that is in the herbarium under this name, because the specimen though a form of *C. alpinum*, nor, of course, *Merendera*, and therefore conflicts with the description of *Species Plantarum*. Consequently the name must be rejected altogether as *nomen confusum*.

The herbarium specimen marked by Linnæus was unmistakably *C. bulbocodioides* Bieb., which replaces *C. Bertolonii* as we go

FIG. 8.



*Colchicum montanum*, Herb. Linn. Natural size.

east, and is specially distinguished by much more numerous and narrower tepals, and by its six-lobed corolla, which is borne on a long pedicel. It flowers from September to November.

Comp. Fl. Gr. iii. p. 274 (1)

The characters of *bulbocodioides* are very evident, as may be seen even in the description of *Colchicum montanum* in the *Species Plantarum*, which has been misapprehended by all the authors who refer to it. Smith's error is evident on the sheet after the words *Colchicum montanum*, « *bulbocodioides* ; » *Bulbocodium* 3. E. b., thong, ft. » (part).



shows that it cannot be a *Bulbocodium* and the anthers that it is not a *Merendera*; both organs are visible and are those of a *Colchicum*. Ascherson and Graebner, Syn. iii. p. 20, quote this specimen for *C. Bertolonii*, which it certainly is not. Bertoloni, Fl. It. iv. p. 277 (1839), says under his *montanum*, which is *Bertolonii* Stev., that "Archetypus hujus speciei ex observationibus Gussonii desideratur in herbario Linnaeno/" an astounding statement to come from such a precisian as Gussone, who had himself dipped into the Linnaean herbarium. But when that author says, in Fl. Sic. Syn. i. p. 437 (1772), "in herb. Linn, species ~~haec?~~ desideratur/" he may only mean that the plant he was at the time describing, which he calls *C. Cupani*, is not to be found in the herbarium: as is the case. On the other hand Visiani, Fl. Dalm. Suppl. p. 36 (1872), and Baker, in Journ. Linn. Soc., Bot. xvii. p. 433 (1879), both attest the existence of the specimen of "*C. montanum*," but the former falls into the error of identifying it with *C. Bertolonii*, while Baker complicates matters, for he identifies *C. bulbocodioides* with *C. montanum* in the sense of *C. Bertolonii*. He was probably unaware of the difference in flowering season, and cannot have noticed the other characters subsequently pointed out so clearly by Boissier and by Halácsy. Then he made a grave mistake in assuming the specimen to be one received by Linnaeus from Loeffling. Of this there is not a shadow of evidence, and three considerations make it impossible: (1) if it were Loeffling's example it would be *Merendera* and not *Colchicum*; (2) it is not like any plant that grows in Spain, where the very distinct *C. triphyllum* Kuntze is the only *Colchicum* besides *C. autumnale*; (3) although there is no indication of origin on the face of the sheet, there is written on the back by Linnaeus, "habitat in Morea."

Thus it appears that there is no connection of any sort between this specimen and the *C. montanum* of the <sup>c</sup> Species Plantarum/ nor indeed would there be any had the example chanced to be really *C. Bertolonii* instead of *C. bulbocodioides*. We cannot, on the strength of the specimen, follow Boissier, *loc.cit.*, in using the Linnean name as equivalent to *C. bulbocodioides* Bieb., for the herbarium cannot take precedence of the <sup>\*</sup> Species Plantarum<sup>f</sup> when there is disagreement. Ascherson and Graebner have unfortunately adopted the same course as Boissier.

I have dealt in more detail with the name *Colchicum montanum* in a recent paper in Nuov Giorn. Bot. It. xxxii. (1875), being no. ci. of my "Piante italiane critiche o rare." I venture to express the opinion that Linnaeus never saw a specimen from Loeffling. Had he seen one we may feel sure that he would not have admitted it as a *Colchicum*. The Linnean Society has a MS. list (Box xvi. no. 7) *manu ignola* of a "Herbarium Loefflingianum; Matriti" in which *Colchicum montanum* occupies no. 176. but Dr. A. Caballero writes from Madrid that he is unable to trace the existence of such a herbarium there at the present day.

Two Rare Spanish Species of *Echium*.

By C. C. LACAITA, M.A., F.L.S.

(PLATE 4.)

[Read 5th March, 1925.]

ECHIUM MARIANUM and ECHIUM PAVONIANUM are only known from single specimens in Herb. Boissier ; through the kindness of M. Beauverd, the keeper of that herbarium, I am able to show a photograph of these, both placed on one sheet for economy of space.

*E. marianum*.—This specimen was referred by DeCandolle in Prodr. x- P- 16 (1846) to *E. fastuosum* (Jacq. f.); but wrongly, as pointed out by Boissier, who published his name of *E. marianum* in Diagn. PL Or. 11, P« 90 (1849). The specimen itself came to him from Dr. Prolongo, of Malaga, who is supposed to have gathered a single individual in the gorges of the Sierra Morena near the Madrid road in the company of *Digitalis mariana*. The label reads :

"*E. marianum* Boiss. ined. in rupibns montis Mariani (Sierra Morena) a cl. Pabl. Prolongo Malacensi collect."

No trace of the plant has ever again been seen by those botanists who have occasionally visited the famous gprge of Despeñaperros. On June 26th of this year, 19J5, I followed the Madrid road right across the Sierra from Santa Elena to Venta de Cardenas, without discovering any sign of the presence of this species. It is to be feared that the label became attached <> a wrong plant, before the specimen came into Boissier's possession. 1^ is impossible in such a case to prove a negative, but for the present *Echium marianum* must be excluded from the flora of Spain.

The case of *E. Pavanianum* is more difficult. The label of this specimen, which came from Herb. Pavon, states that it grew at Aldeguela, and was most abundant there in September 1806, so it should not be difficult to rediscover the plant if we knew what village is meant by "Aldeguela." Unfortunately there is no place in Spain of that name, as DeCandolle, <sup>loc\*</sup> dt., remarks in a note: "Aldeguela in lexicis geographicis deest et <sup>origo</sup> non certe hispanica." Boissier, on the other hand, says "Hic <sup>loc</sup> us mihi ignotus est sed ex schedule forum comparatione in provincial <sup>extremadurd</sup> probabiliter situs." Now, although there may be no such place as Aldeguela, the Spanish gazetteer records no less than 33 of the very similar name of Aldehuela, a word which literally means "hamlet;" Of these, three are in Extremadura and three more in the adjacent province of Salamanca. I have been close to Aldehuela de la Boveda and Aldehuela

de Yeltes in the latter district; both lie in cultivated land where the presence of such an *Echium* is very improbable, and if it grows most abundantly one could hardly overlook it.

As to the three Aldehuelas in Estremadura; the same remark applies to the one which I have visited—I do not think any one else has been there—on the right bank of the river Jerte, some 10 miles S.W. of Plasencia. Another is in a remote part of the Hurdes, the wildest and most inaccessible corner of Spain ; it is described in an old gazetteer as lying at the foot of the Puerto de Esparaban, and consisting of 25 cabins (in the Irish meaning of that word). It is incredible that Pavon should have visited such a spot, which even to-day is some 30 miles by rough mountain tracks from the nearest highroad. I penetrated some distance into the Hurdes, from the old deserted monastery in the lovely glen of Las Batuecas, but did not get within 12 miles of Aldehuela. The flora of these grim hills of the Hurdes seems to be extremely poor and very uniform, being mostly composed of sundry species of *Erica* and *Cistus* or *Halimum* mixed with *Arbutus Unedo*. There is an interesting account of this very little known district in Aubrey Bell's 'Pilgrim in Spain' (1924).

I could not find time to visit the third Aldehuela in Estremadura, which is more accessible, lying not far from Caceres. This one offers the best, if not the only, hope of rediscovering Pavon's plant, but I confess to some scepticism as to its existence in Spain ; the habitats assigned in Pavon's labels are not always to be trusted. Witness the case of *Marrubium hispanicum* ex Herb. Pavon in Mus. Brit, mentioned in my recent paper on *Atarrubium* and *Ballota* in this Journal (*supra*] p. 169).

The label of *E. Pavonianum* reads :

<p>" Echium Aldeguela abundantis.<sup>m?</sup> Sepfe de 1806 Hispania. Herb. Pa von."</p>
---

#### EXPLANATION OF PLATE 4.

Fig. 1. *Echium Pavonianum* Boiss.

Fig. 2. *Echium marianum* Boise.

Both from photographs by M. Beauverd, Herb. Boissier.

July 23, 1926.

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# THE JOURNAL OF THE LINNEAN SOCIETY.

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**Previous Investigations into the Distribution and Ecology of Marine Algae in Wales. By KENNETH REES, M.SC. (Communicated by Dr. FLORENCE MOCKERIDGE, F.L.S.)**

[Read 23rd April, 1925.]

IN the course of an investigation into the ecology of the Phaeophyceae of the coast of Wales, it was suggested that attention might be paid to the scattered published records of those who, either resident in Wales or visiting its shores, had been gradually building up our present knowledge of its marine flora. The present account, therefore, is an attempt to gather together, from the various sources enumerated in the list of references, material sufficient to compile a chronological account of the development of marine algology in Wales. A list of the seaweeds recorded is retained in manuscript form and is based upon the classification adopted by Batters in his \* Catalogue of British Marine Algae, 1902.

**Period 1500-1650.**

Though this period may be termed the age of the herbalists it may be noted that, following upon the Renaissance and the re-interpretation of Theophrastus and Dioscorides, attempts were made to arrange, in sections, the plants then known. For marine species the terms "Ulva" and "Fucus" were adopted. In Wales, 'Meddygon Myddfai' with its catalogue of "the names of the herbs, fruits and vegetable substances which every Physician ought to know," was composed and was the basis upon which Dr. John Davies (1570-1644) wrote his 'Botanologium' in 1632 (9). References occur in both to "gwimon," "gwig mor," "dylysg y mor," "ysnodcn y mor," as Welsh equivalents of Alga or Diva.

The 'Botanologium' \* was the forerunner of a number of similar catalogues or lists of plants appearing from time to time in Welsh-English dictionaries (12,13,14,15). Of a number of herbals written in Welsh during this period, the most noteworthy is that of William Salesbury (1520-1600) (\*6). Towards the end of the period, Thomas Johnson (d. 1644) a Yorkshireman, who in 1639 visited Wales but recorded no marine plants, published his edition of Gerard's 'Herbal' in a reprint of which in 1636 (36) there occurs a list of Welsh plants sent by Robert Davyes of Guissanay, Flintshire. But neither in this list nor amongst Johnson's marine plants (37) is there a definite reference to a seaweed from the coast of Wales.

### Period 1650-1725.

With the publication of How's \* *Phytologia Britannica*/ in 1650, followed later by Ray (59, 60, 61), a systematic classification was being attempted and the first reliable records of marine algae in Wales can be sought. During August 25th-September 7th, 1658, John Ray (1627-1705) made his first itinerary through North Wales (48). He touched the coast at Aberconway, Penmaenmawr, Bangor, Menai Bridge, Beaumaris, and Dolgellau. Four years later, during May and June, accompanied by Francis Willughby, the Ornithologist, he made his second itinerary, entering Wales at Wrexham, encountering the sea-board at many places along the north coast, and in Anglesey, as well as at Abordaron, Pwllheli, Harlech, Aberdovey, Cardigan, Fishguard, St. Davids, Tenby, Laugharne, and Kidwelly, before leaving via Chepstow.

In his diary there are many references to sea-birds, fishes, and maritime flowering plants, but it is only from the internal evidence of his 'Synopsis' (59) that conclusions regarding records of marine algae can be drawn. Of *Padina pavonia* Gaill., he writes "ex insula Anglesey et Cornubiensi"; of *Laminaria digitata* Lam., "Vidimus etiam rupibus marinis aqua pleno mari inundantis copiosissime adnascentum circa Monam insulam" (Note, Vidimus=we saw, *i. e.*, Willughby and Ray). In this work there are several citations of "D. Lhwyd." Edward Lhwyd (1670-1709) explored Wales in 1688 and 1693 to collect in the first instance for the Ashmolean Museum, of which he was Keeper, and in the second for Dr. Gibson's edition of Camden's 'Britannia' (11). He also sent many specimens to Ray for his 'Synopsis' and to Dillenius for his third edition of this work. He made further visits in 1826 and later, with Dr. Richard Richardson as companion. In Ray's \* 'Synopsis' he is credited with *Laminaria saccharina* f. *Phyllitis* Le Jol. and *Fucus spiralis* f. *platycarpus* Thur. Of the former, Lhwyd states: "This in Welsh is called 'Mor Dowys,' the poor people eat the small leaves and clusters as they do 'Delesh' (*Rhodymenia palmata*); the larger are found sometimes two feet long." It is interesting to note that in his 'Archseologia Britannica' (1707), Tit. II., he mentions as examples of "Alga" (Welsh "Gummun," Irish "Duileasg") *Dilsea edulis* Stackh. and *Laminaria digitata* Lam. In Gibson's edition of Camden's 'Britannia' (1695), for which it is so often stated that Lhwyd collected, no marine algae are mentioned save *Ulva Lactuca* L., concerning the use of which in making "Lhaivan" or "Laver bread" a detailed account is given in the section dealing with St. Davids (22, p. 765).

### Period 1725-1760.

This is the period of the pre-Linnean systematists typified by Dillenius in Great Britain. In 1726, during the latter part of May, Littleton Brown (b. 1669) of Bishop's Castle made a short journey through South Wales,

of which an account is given in a letter to Dillenius (75, p. lxxiii). He visited the shore at Cardigan, St. Davids, St. Brides, Pembroke and Tenby, but his records are all of flowering plants. However, during a later journey in July 1731, he collected "sea plants. . . . some new, especially among the Confervas which came all from Aberystwyth, my journey last July" (75, p. lxxv). Amongst them is *Ahnfeltia plicata* Pries. During late July and throughout August 1726, Dilleniui (1684-1747) and Brewer (c. 1700-1742) made a journey into North Wales. Though in the diary of their journey the only reference to marine vegetation is to "two new sea mosses from rocks washed by the sea over against Prestholm I.," it is clear from his herbarium (75) that Dillenius collected many seaweeds during the visit. In all, he records three Blue-Green, eight Green, seven Brown, and twenty-five Red seaweeds, nearly all from Anglesey. Brewer, who remained at Bangor till May 1727, kept a diary of his excursions, but his references to marine algae are usually of a general character, e. g., in writing of Porthaethwy (Menai Bridge), "I never saw before so grand a variety of Confervas, Corallinae, and Fucoides as I found in this place, nor so pleasant a sight as the variety of colour and structure in one hole or pool." The Pools to which he refers are those on the rocky island of Ynys-y-moch, a name which occurs often in his records of marine algae. Again, "On the Rocks called Trwynhir. . . . several curious Confervas, Fucoides, and florallitæ.

References to particular plants do, however, occur, e. g., "at Trwyn-y-clegin; found in great plenty *Fucus phyllitidis folio* (= *Laminaria saccharina* f. *phyllis* Le Jol.), or 'Mor dowys/ and great plenty of a Fucus that is called in Wales everywhere 'Dillesh' (*Dilsea edulis* Stackh.) and a great many seedling plants of sea-laces (*Chorda Filum* Stackh.)." But, as in the case of Dilleniui, it is from a study of the latter's herbarium that the extent of Brewer's discoveries can be estimated. In his name, two Green, three Brown, and twenty-eight Red seaweeds are recorded, not necessarily different from those of Dillenius himself, twelve being recorded by both (75).

Both in Brewer's diary and in the labelling of the Dillenian herbaria mention is made of Mr. Green, a young clergyman who appears to have resided at Holyhead. He sent many plants to Dillenius (75, pp. lx, lxxiii), and accompanied Brewer on some of his excursions. *Ilimanthalia lorea* Lyngh. and *Ascophyllum nodosum* Le Jol. are recorded in his name. He is mentioned, along with Brewer, as the authority for *Fucus ceranoides* L., *SaMorhiza polyschides* Batt., *Phyllophora membranifolia* J. Ag., *Plumaria elegans* Schm., *Delessaria alata* Lam., and *Ahnfeltia plicata* Fries. Other local botanists mentioned include William Jones, who acted as a guide to Brewer and accompanied Dillenius to Penmon and Llanfaethly, whence three seaweeds are labelled on his authority; Thomas Price, the conjuror, of whom Brewer writes "he brought me from the weirs he renteth of the Bishop of



Bangor, called Ynys-fadoc-goch, an olive coloured sea garlic, a yellow branched seaweed—it appeared round and tubulous" ; and Dr. Foulkes, who not only aided Lhwyd when in North Wales, but sent to Dillenius a number of specimens from his private collection, including the two algæ—*Cystoclonium purpureum* Batt. and *Ceramium rubrum* Ag.

### Period 1760-1824.

In 1753 Linnaeus published his 'Species Plantarum' and for nearly seventy years botanists followed the Linnean system of nomenclature and classification. Amongst the first in Britain was William Hudson (1730-1793), who published his 'Flora Anglica' in 1762. As to whether he visited Wales, information is inadequate. In both Withering's 'Arrangement' (79) and Turner and Dillwyn's 'Botanist's Guide' (74), plants are recorded for Welsh localities upon the authority of Hudson, who, in his 'Flora Anglica,' either cites Dillenius or Lhwyd, or gives no authority at all for such plants. Only by assuming that these plants quoted without authority are the results of his own observations, may it be suggested that Hudson visited Wales, in which case the visit would be prior to 1762.

In 1773, Rev. John Lightfoot (1735-1788) accompanied by Sir Joseph Banks (1743-1820) visited Wales (40, vol. xliii. p. 290). The tour extended from June 25th to August 16th, several weeks being spent in Pembrokeshire. The coast-line was reached at a number of places, e.g., Nash Point, Briton Ferry, Freshwater Bay East, Tenby, Penally, and St. Davids in South Wales ; and Abergele, Menai Bridge, Llanddwyn, Llanfaelog, and Cemlyn Bay in North. Maritime flowering plants and ferns are frequently mentioned, but no marine alga). However, in 'The British Flora' by John Hull (1799), *Maria esculenta* Grev. is recorded for Holyhead upon the authority of Lightfoot.

Before the next visit, that of John Stackhouse in 1796, there appeared Gough's edition of Camden's 'Britannia' (1789). In a prefatory note the editor writes : " A formal catalogue of plants . . . has, I trust, been in some measure supplied by the help of some young friends who have exerted their utmost diligence in collecting the plants peculiar to each county from books and from the researches of themselves and other botanists who have multiplied since Ray in the same proportion as the Science has improved." The only Welsh county for which marine algæ are recorded is Anglesey :—one Blue-Green, two Green, six Brown, and three Red, of which all, save *Cladostephus spongiosus* Ag. and *Fucus vesiculosus* L., had been previously mentioned by Dillenius or Brewer.

Stackhouse (1742-1819), whose 'Nereis Britannica' appeared in 1801, visited Tenby. Describing *Fucus Opuntia* (= *Catanella repens* Batt.) he writes:—" Specimen hanc rupibus adnascentem juxta Tenby oppidum in Wallia Australi, A.D. 1796 detexi." He also records *Fucus Phyllitis* (= *Laminaria saccharina* f. *Phyllitis* Le Jol.) at the same place.

During the period 1797-1804, a number of pedestrian tours through both North and South Wales were undertaken by persons with a greater interest in history and archaeology than in Botany (1, 4, 10, 19, 20, 67, 76, 78). In their diaries or published works, however, a few noteworthy records appear. John Evans, "accompanied by persons calculated to give assistance to inquiry and stimulus to research," entered upon a journey into Wales in the summer of 1798. At Traethvychan, near Harlech, the appearance of two *Cladophoras* seems to have attracted his attention. "Swimming like the little Nautilus upon the bosom of the waves appeared *Conferva vagabunda* (= *Cladophora fracta* Ktztz.)." "Let the doubting Naturalist watch . . . . the Peking and veering of the vegetable mariner *Conferva jtegagrophila*" (p. 139). Several references to "Corallines and Fuci" occur in descriptions of a rocky foreshore (20, p. 337), but flowering plants form the bulk of his botanical observations. At St. Davids he describes the method of making Llaivan (Laver bread) from *Viva lactuca* and *Ulva umbilicalis* (= *Rhodymenia umbilicalis* Ktztz.) in words almost identical with those employed in Gibson's Camden's 'Britannia' (20, p. 299, cf. 22, p. 765).

Of a similar character was the tour of Arthur Aikin in 1797. Though primarily a mineralogist he frequently gives lists of flowering plants. His references to marine algae are of a vague and general nature. Writing of Aberystwyth, for instance, he states;—"Northwards of the castle is a level beach, a few hundred yards in length, to which succeeds a long range of high slate rocks. . . . at the foot of these cliffs extends a reef of low rocks covered at high tide, the crevices and pools of which are adorned with numerous beautiful corallines and fuci" (1, p. 47). None, however, are described.

In 1805 appeared Turner and Dillwyn's \*Botanist's Guide/ Marine algae recorded for Anglesey (seventeen Fuci, five Ulvse, ten *Conferva*), Carnarvonshire (one *Conferva*), Denbighshire (two Fuci), Glamorganshire (eleven Fuci, five Ulvse, ten *Conferva*), Pembrokeshire (three Fuci). The authorities quoted are :—Anglesey, Rev. H. Davies and Dillenius ; Carnarvonshire, Dillenius ; Denbighshire, J. W. Griffith ; Glamorganshire, Dillwyn ; and for Pembrokeshire, Dillwyn and Stackhouse, It is somewhat remarkable that Dawson Turner (1775-1858), whose 'Synopsis of the British Marine Algae' appeared in 1802, made no reference to those growing on the coast of Wales. In the 'Synopsis' all the Welsh records are upon the authority of Hugh Davies, except *Fucus palmatus* (= *Rhodymenia palmata* Grev.) and *Fucus siliquosus* (= *Halidrymnia siliquosa* Lyngb.), which are mentioned as "not uncommon" on the shores of England, Wales, and Scotland. Though in the preface to the 'Botanist's Guide' it is stated that Turner is responsible for the Cryptogams, in so far as the Welsh counties are concerned, it is mostly for flowering plants that his initials appear as authority. Dillwyn (1778-1855), however, added considerably to

our knowledge of the marine algae, especially of the Swansea district. In his 'British Confervae' (1809) there are thirty-one Welsh records, mostly upon his own authority. These, together with those found in the 'Botanist's Guide' in Withering's 'Botanical Arrangement' and in Gutch's list in the 'Phytologist' (vol. i. p. 184), bring the total number of marine algae appearing in his name to ten Green, ten Brown, and twenty-three Red species.

Two minor Welsh botanists of this period were William W. Young, who is described by Dillwyn as "an ingenious artist at Swansea," and John Wynne Griffith, of Garn, Denbighshire. Young executed most of Dillwyn's plates for the 'British Confervas' and his name appears as authority for seven marine algae from Newton Nottage, Dunraven Castle, and Laugharne. Griffith, who is mentioned in terms of high praise by Withering in the prefaces to various editions of his 'Botanical Arrangement' appears as the authority for two Fuci (*Desmarestia ligulata* Lam. and *Dilsea edulis* Stackh.) mentioned for the county of Denbighshire in the 'Botanist's Guide.'

In 1813, Rev. Hugh Davies (1739-1821) published 'A Welsh Botany' a comprehensive flora of Anglesey, containing an excellent list of algae under the headings "Fucus" (fifty-eight, all marine), "Ulva" (twenty-five, of which twenty-one are marine), and "Conferva" (eighty-six, of which forty-two are marine). An analysis of this list and of references to Davies in contemporary algal literature (17, 24, 26, 33, 42, 70, 73, 74, 79), brings the total of his records to two Blue-Green, eighteen Green, thirty-two Brown, and fifty-eight Red species. He appears to have been frequently consulted by Turner, Goodenough, and Woodward, upon critical species or points of nomenclature.

### Period 1824-1878.

With the publication in 1824 of C. Agardh's 'Species Algarum' the natural system, as the basis of classification, was extended to marine algae. When therefore, John Baits, of Penzance, visited Wales in 1841, a new nomenclature was in force and the algae he recorded can be identified with greater accuracy than is possible in the case of previous investigators. Ralf<sup>s</sup> visited Wales again in 1842 and several subsequent years, and in 1842 was accompanied by William Borrer, a Sussex algologist. In all, he recorded eight Blue-Green, seven Green, nine Brown, and twenty-two Red seaweeds (26, 55, vol. i. pp. 193, 490, and 184). Ralfs was the first botanist, who had made algology a life-study, to visit Wales, and his records amongst the smaller species are of considerable interest. His journeys, too, extended over a wide area, the coastline from Swansea, the Gower and Milford Haven in the south through Aberystwyth, Barmouth, and Dolgellau in Cardigan Bay, to Carnarvon, Bangor, Menai Bridge, Holyhead, and Aberffraw in the north, being carefully explored.

Both Harvey (26) and Ralfs mention Rev. T. Salwey, of Oswestry. He recorded *Taonia atomaria* J. Ag. at Tenby, and *Nodularia spumigena* f. *litorea* Born. & Flah. at Barmouth, at a date prior to 1843.

In 1844, J. W. G. Gutch, of Swansea, contributed to 'The Phytologist' (vol. i. p. 184) a list of plants in the neighbourhood of Swansea. The list includes a catalogue of marine algae. Apart from two citations of Ralfs and a repetition of Dillwyn's records in the 'Botanist's Guide,' the list appears to be the result of Gutch's own observations, which total eleven Green, fourteen Brown, and forty Red species.

A local list of the same character is that of Thomas Owen Morgan of Aberystwyth. In 'Flora Cerevica Superioris' (1849), under the heading 'Aberystwyth,' he writes:—"The rocks extending from the beach at Aberystwyth towards the west are covered every tide at high water, but at low water become exposed to view and form pools and crevices which furnish the collector with a variety of algae and corallines for preserving. The following list of marine plants found there may, for that purpose, prove useful." The list comprises five Green, twenty-three Brown, and twenty-eight Tied seaweeds. As the list includes *Himantalia lorea* Lyngb., *Saccorhiza volyntiosa* (L.) Mont., *Sporochnus pedunculatus* Ag., and *Dictyopteris membranacea* (L.) Mont., none of which are found there to-day, one may conclude that either a remarkable change has taken place in the local marine flora or that Morgan's observations did not err on the side of accuracy. Morgan also produced a 'Guide to Aberystwyth' with a list of flowering plants, an example followed by several later compilers of "Guides" (7, 35, 38, 51, 64). None, however, contain lists of marine algae.

### Period 1878-1920.

The studies of Bornet and Thuret on sexual fertilization (1878) may be said to mark the beginnings of modern marine algology. Algologists turned their attention from mere collecting for herbaria to a critical study of marine species, their morphology, cytology and, more recently, their ecology and physiology. One effect of this has been to limit records to a few species or families in which the observer was interested. Thus Dr. J. E. Gray, in a note on *Desmarestia* (40, vol. iii. p. 171) writes:—"In Wales I have found these two plants (*Z. ligulata* Lam. and *D. viridis* Lam.) growing apparently from the same root-disc." This was probably in 1865. In April 1881, E. M. Holmes visited North Wales and found *Phaeospora mbarimlata* (= *Stictyphion subarticulatus* Hauck) at Carnarvon (21, vol. ii. p. 142), either then or during a later visit he recorded several other species in Anglesey or Menai Strait (25, 40, vol. iii. p. 250), and at a meeting of the Linnean Society in March 1911 exhibited *Griffithsia globifer* J. Ag. from Milford Haven. In 1885, during the latter part of June, Dr. O. Nordstedt

visited Wales and recorded *Symploea atlantica* Gom. at Ferryside, Carmarthenshire (21, vol. xxii. pp. 22 & 51), and *Vaucheria litorea* Bang, et Ag between Dolgellau and Barmouth (66, p. 382). In 1886 (21, vol. xv.) and 1890 (81, vol. xxii. p. 91) E. A. L. Batters came to North Wales, and, judging by records in his 'Catalogue of the British Marine Algae' (1902), he botanised chiefly at Point of Ayr (Flintshire) and Puffin Island, though, in addition, there are records for Rhyl, Bangor, and Holy head. He added eight Blue-Green, six Green, five Brown, and six Red species to those previously recorded.

In 1914, A. D. Cotton, studying the ecology of *Ptilota phmosa* Ag, *Callitliamnion arbuscula* Lyngb., and *Codium mucronatum* f. *atlanticum* wh visited Barmouth, Aberystwyth, Fishguard, Strumble Head, Newport, and Dinas Bay. He failed to find these three species, but notes the *Nemalio* and *Callitliamnion* associations at Dinas Bay and *Porphyra* association at Newport (40, vol. lii. p. 35).

In addition to these somewhat scattered records, there appeared during the last decade of the 19th century three notable contributions towards a complete list of marine algae for the coasts of Anglesey and Carnarvonshire. The first was that of R. J. Harvey-Gibson. In the 'Proceedings of the Liverpool Biological Society,' vol. iii. (1889) and in Report III- or the Liverpool Marine Biological Station (1892), he published lists of marine algae for many areas including Anglesey and Puffin Island. In all, fifty Blue-Green, thirty-two Green, fifty-six Brown, and ninety-four Red seaweeds are recorded.

The second appeared in 1895 in John E. Griffith's 'Flora of Anglesey and Carnarvonshire,' and contained seven Blue-Green, twenty-two Green, forty-three Brown, and ninety-nine Red species. Lastly, in 1896, Professor R. W. Phillips published a list of sixty-one Brown seaweeds (54) gathered, those of Griffith, from many localities in the Menai Strait and Anglesey.

Since that date, apart from a very incomplete list for Aberystwyth, there has been no further contribution to our knowledge of the distribution of marine algae on the coast of Wales.

The records of the investigators whose activities have been described are brought together in a manuscript list, which comprises thirty Cyanophyceae, forty-eight Chlorophyceae, eighty-five Phaeophyceae, and one hundred and thirty-eight Rhodophyceae, a total of three hundred and one species, confined, however, very largely to four coastal areas:—Anglesey (including Menai Strait), Aberystwyth, Pembrokeshire, and the Gower.

In conclusion I would wish to express my thanks to both Prof. R. W. Phillips of Bangor and Prof. J. Lloyd Williams of Aberystwyth for their kindness in allowing me to read private copies of books and manuscripts, and to the latter for many helpful suggestions and criticisms.

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A Critical Study of certain Species of the Genus *Nmropteris* Brongn.

By EDITH BOLTON, M.S.C, F.L.S. Bristol Museum.

(PLATE 5 & 6, and 5 Text-figures.)

[Kend 5th November, 1925.]

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1. INTRODUCTION.

EARLY in 1920 the writer, whilst working on the Coal-Measure Plants of the Northumberland and Durham Ooalfield, collected material from a band of ironstone nodules occurring in brick clays at th. . . . . rks, Crawcrook, Go. Durban. The nodules proved to be ucl<sup>1</sup> in plant-remains, and particularly in species of the S ^ ^ X Z 'noS. . . . . of specimens these specimens proved difficult, owing to the large num<sup>1</sup> of apparently intermediate between recorded H<sub>2</sub>£- . . . . . forms, which these intermediates occurred suggested that they quite as much so as the usually accepted species. This discovery of wight dearly seemed to be stable intermediates between J<sup>1</sup> j j ^ hitherto as species led me to investigate more closely the whole, q Q£ what forms owed their supposed specific characters to the portum they occupiea «pon the rachis or to conditions of development. iulBnBediato> occur

Subsequent research has shown that *is europteris* throughout the coalfields of England.



This paper contains the results of investigations into the question of **what** forms may be retained as valid species and what as intermediates. **The** character and development of the different modes of pinnule growth **M** different parts of the frond are also considered.

## 2. REMARKS ON THE GENUS *NEUROPTERIS*.

1822. *Filicitea* (Section *Neuropteris*) Brongniart, Classification des Végétaux fossiles, p. 33.

1826. *Neuropteris* Stenberg, Essai flore du monde primitif, vol. i. fasc. iv. p. 10.

1828. ——— Brongniart, Prodrôme, p. 52.

1886. ——— Zeiller, Flore fossile du Bassin houiller de Valenciennes, p. 249.

### *Diagnosis of NEUROPTERIS.* (Brongn., 5, p. 226.)

"Folia bipinnata, vel rarius pinnata, pinnulis basi saepe subcordatis, nec inter se nec rachi integre adnatis, sed parte media tantum insertis; nervo medio apice evanescente; nervulis obliquis arcuatis tenuissimis dichotomis."

Members of this genus were large plants bearing enormous fern-like fronds, some of which bore seeds (Kidston, in Phil. Trans. Roy. Soc. Edinburgh, vol. exvii. (1904) pp. 1-5), a fact which at once clearly separates them from true Ferns. "The fronds were probably tripinnate as well as bipinnate. The principal rachis bifurcated at a more or less wide angle, and the pinnae arising near the angles of bifurcation were much less developed and less cut up than were the external pinnae, being often only simply pinnate when the latter were bipinnate. There was therefore a notable disparity between the two sides on the same portion of the rachis" (Zeiller, 20, p. 249).

The *Neuropteris* pinnule, with few exceptions, has the margin entire, and the surface of the lamina smooth, except *N. Scheuchzeri* Hoffm., where the surface is covered with fine hairs. The apex varies from round to acute, and the venation, except in *N. rarinervis* Bunbury, does not vary much in density. The amount of overlap of the pinnules varies much, being influenced partly by environment and partly by fossilisation.

### *Validity of certain Species.*

That some of the earlier workers were doubtful as to the validity of certain species is evident from their writings. Brongniart (5, p. 237) even expressed doubt about the validity of some of his own species. Bunbury says: "I must observe that the number of described species is probably far too great, and that the greater proportion of them would probably be found, if completely known, to be variations or modifications of a few real specific types. Many of them have been described from very imperfect specimens, often, indeed, mere fragments. Now, in those kinds of *Neuropteris* which are best known we see that (as in many ferns) the size, outline, and position of the leaflets vary very much in different parts of the same frond. In

making n ^ '» therefore, of such imperfect material as we most often have before us, in the case of fossil plants, we are exceedingly liable to create false species, and to describe under several distinct names different fragments of the same material. This statement abundantly has in a large measure proved to be correct.

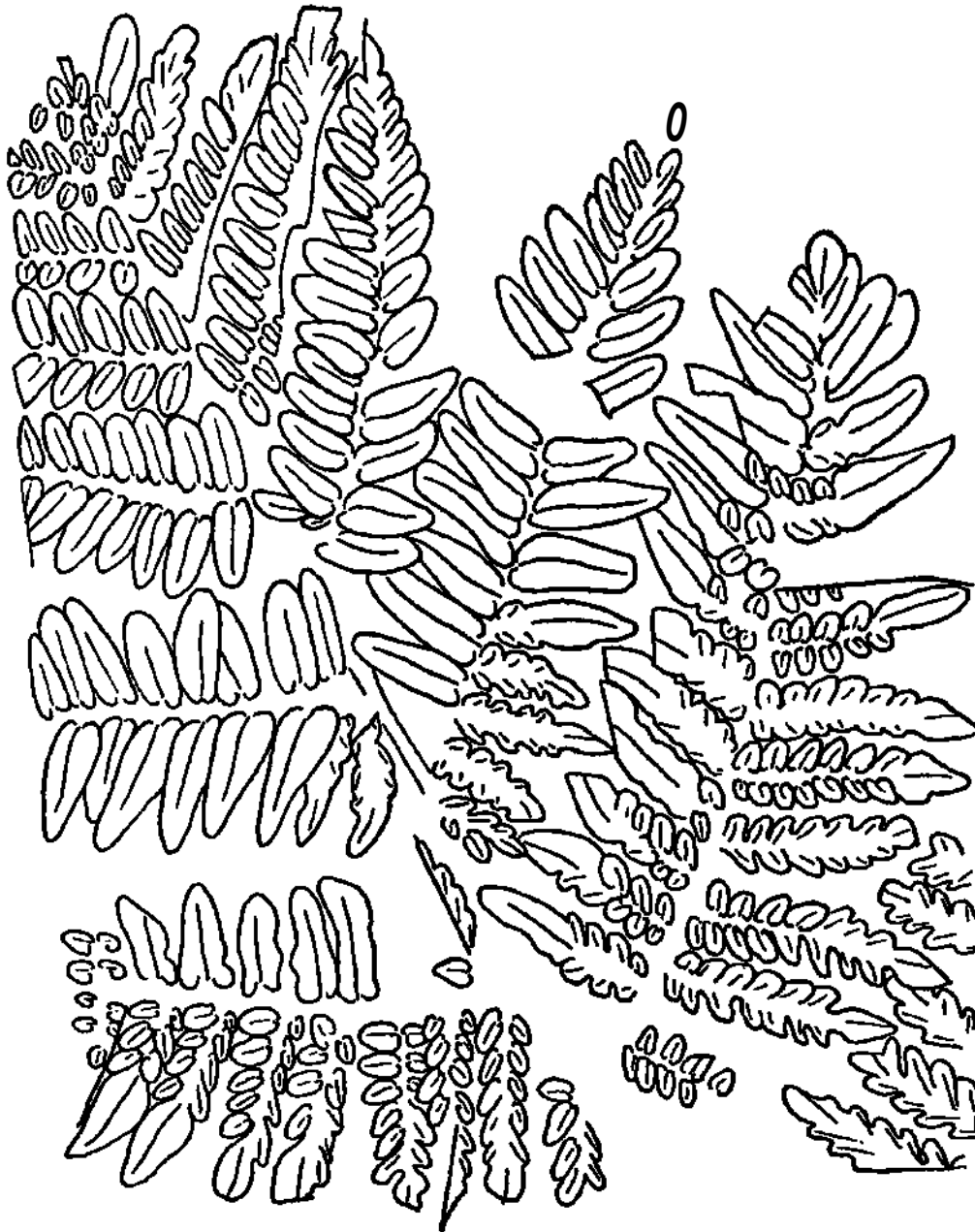
3. DIAGNOSTIC CHARACTERS.

def U ^ In this connection become evident that it was necessary to determine what features could be considered as constituting adequate diagnostic characters. Kidston and Zeiller regarded the number of veins entering a centimetre of leaf-margin as a satisfactory diagnostic character. The result of the count of veins per centimetre by us, counted on a large number of specimens, shows that there is not sufficient constancy of veins per centimetre to make this of any great value. The reason for this inconsistency is that no new veins are produced by a leaf after its development in the bud, the only growth which takes place is in the lamina itself, result of this as a result of growth of the tissues between the veins. As a number of veins entering a centimetre in a mature leaf is less than those entering the same area in an immature leaf. Therefore it is not possible to employ the number of veins entering a centimetre of leaf-margin as a diagnostic character, unless the leaves be of the same age. Both Kidston and Zeiller have used this as a diagnostic character, and it has led to a certain amount of confusion between the species. Owing to the failure of this character there remain those of size and shape. Very few of the specimens realized the fact that the sizes of the pinnae and pinnules are dependent to a large extent on their age and position on the plant. Consequently a number of specimens closely resembling certain species in size and shape have not been referred to these species by Brongniart and others, solely because of size-difference (Zeiller, 20, p. 277). A large extent of the characters must be taken into account when identifying specimens of Neuropteris. That Neuropteris fronds were not always homophyllous but were also frequently heterophyllous is evident when large portions of fronds are found, a good example is seen on the specimen figured by Zeiller (20, p. 43), a fragment of which is given in text-fig. 1. Many of these heterophyllous forms are, I am certain, to be found amongst specimens now identified as N. heterophylla Brongn. There is abundant evidence, as will be seen later, that N. heterophylla Brongn. has

become a somewhat "omnibus" species, to which is relegated quite a number of variants and intermediates of other species.

The determination of the mode of development of pinnules and their probable position on the frond has formed the chief basis of determination of

FIG. 1.



Heterophyllous fronds of *Neuropteris* after Zeiller (reduced).

specific character in this paper. Thus, in identifying a specimen of *Neuropteris*, it was first necessary to consider its probable age (whether immature or fully grown), its relation to the rest of the pinna, and the probable relation of that pinna to the frond. It is only by a careful consideration of these factors that a specimen can be correctly identified.

By adopting the above methods, we are now in a position to restate the

characters of most of the common British Ool-Measure species of *Neuropteris*, and to indicate more clearly the detailed features of frond development. It will be further shown that it is possible for the known species of £ « « \* \* « . to be brought together into "species-groups" (Gregory, 8, p. *il*). these species-groups will now be described in detail.

4 A. Species-group N. FLEXUOSA.

NEUOPTERIS FLEXUOSA Sternb.

1823. *Neuropteri, Jlexuo*^ Sternberg, Flora der Vorwelt, Vers. i. fuse, iv. p. 10; Vers. n.

1826. *Nj^'ris omta* Hoffmann, in Keferstein's T.utschland geognostisch-geologisch

1800 ^ r ^ B ^ C i ! £ £ £ ' \* « \* » \* \_ \* \* 239, pl \_ ^

1800. — " ^ S i ^ ' S a i t e - d e P a K o n t o l o g i e V ^ t a l e , v o l . i . p . 434, pl. 30.  
figs. 12, 13.

1870. — U ^ r , p r i m a s v a l W o r l d o f S w i t z e r l a n d , v o . . . p . 10.

1880. — Zeiller, Flore fossile du Bassin houiller de Valenciennes, p. 277, pl. 46.

1823. *Neuropteri. plicata* Sternberg, Flora der Vorwelt, Vers. i. fasc. iv. p. 16; Ve».ii.  
p. 74, pl. 19, figs. 1 & 2.

1830. — Brongniart, Histoire des V6get>ux fossiles, p. 148.

1859. *NeuropterU rotun\*folia BwUry*, in Quart. Journ. Geol. Soc. London, vol. xiv.

1823. O , « « ^ i 2 ! var. ft Sternberg, Flora der Vorwelt, Vers. i. pp. 36, 39, pl. 32.

1830. *Neu^'rU keterophylla* (in part) Brongniart, Histoire des V6getaux fo<iles,

1880. - J ' ! ! ! : Zeiller> F l o r e fosrile du Ba.sin houiller de Valenciennes, pis. 43, 44,

1830. A i w r o p S i L o s h i i Brongniart, Ilutoire des V6g6taux fosses, p. 242, pl. 62. fig. 1,  
pl- 63.

1830. *Neuropteris Soretii* Brongniart, *ibid.* p. 244, pl. 70. ng. 2. . . .

1823. *Neuropteris thymifolia* Sternberg, Flora der Vorwelt, Vers. ii. p. 76, . . . 74.

1830. *Neu^'teri, - L o r t i e U d . . Brongniart, - H i s t o i r e d e s V 6 g 6 t a u x f d s s i l e s* p. - 44, pl.

1887. *N J % £ v O B a t a K i d s t o n*, in Proc. Itoy. Soc. lidin. vol. xxxiii. pt. ii. (1887J,  
p. 369, pl. 22. fig. 1.

Remarks on synonymy of NKUROI>TEIUS FLEXUOSA Stend>.

N . ^ E X U O S A .

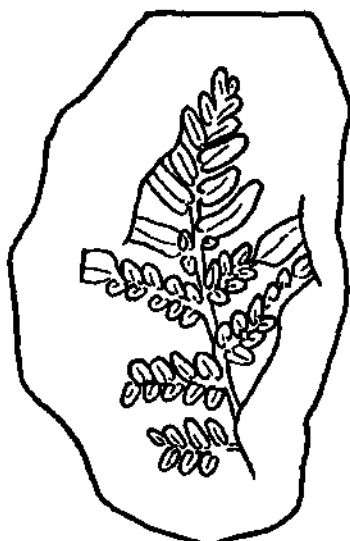
C « e f u l e x a m i n a t i o n o f a l a r g e n u n . b c r o f s p e c i m e n s i n v a r i o u s c o l l e c t i o n s  
h a \* P r o v e d t h a t a n u m b e r o f i m m a t u r e s p e c i m e n s o f *I T . f l e T M \* \* \* & « \* £*  
*l' \* «* g r o u p e d w i t h o t h e r s p e c i e s u n d e r t h e s p e c i f i c n a m e . *N > £ » £ \* £*  
J ^ g n . B r o n g n i a r t h i m s e l f ( 5 , p . 243; s t a t e s t h a t i t i s d i f f i c u l t t o d \*  
H u i s h s o m e f o r m s o f *J f . h e t e r o y h y l l a* B r o n g n . f r o m o t h e r j J L k « m n  
8 ^ 8 . T h i s d i f f i c u l t y w a s p r o b a b l y d u e t o t h e f a c t ^ . " 1 « \* B J . \* £  
d i d \* > t m a k e s u f f i c i e n t a l l o w a n c e f o r g r o w t h c h a n g e s . F o r i n s t a n c e , Z e i l l e r

(20, p. 277) says that *N. flexuosa* Sternb., although closely resembling certain forms of *JV. Iteterophylla* Brongn., is distinguished from it by the fact that it is never found so small. He failed to realise that his *N. flexuosa* pinn<sup>\*</sup> might be but the mature stage, and certain forms of *JV. heterophylla* He mentions, the smaller immature stage of one and the same species.

#### NEUROPTERIS LOSHII.

The specimens figured by Brongniart (5, pi. 72. fig. 1 & pi. 73) of which pi. 72. fig. 1 is reproduced as text-fig. 2, under the name *Neuropteris Loshii* Brongn., are clearly only the immature forms of *N. flexuosa* Sternb. The type-specimens of this species (*JV. Loshii* Brongn.) came from the Newcastle Coalfield, an area in which *JV. flexuosa* Sternb. is very common, an

FIG. 2.



*Neuropteris Loshii* after Brongniart (reduced).

these two species are frequently found in close association. Brongniart further remarks upon the resemblance between *JV. Loshii* Brongn., *JV. tenuifolia* Schloth. (sp.), and *JV. flexuosa* Sternb., but suggests that the chief difference lies in the size, character of venation (being thicker and more compact in *JV. Loshii* Brongn.), and also in the less caducous nature of the pinnules of *JV. Loshii* Brongn. These are all characters which are, to a great extent, governed by age, growth, and position on the rachis.

Bunbury (7, p. 248) says that after careful examination of a great number of specimens, he is unable to satisfy himself, owing to the occurrence of intermediate forms, that *JV. flexuosa* Sternb. is permanently distinct from *JV. gigantea* Sternb. He also considers that the overlapping of the pinnules in the former species, a character on which Brongniart lays great stress, is not to be relied on. My observations are in agreement with Bunbury. Heer (9, p. 10) suggests that such forms as *JV. gigantea* Sternb. and *JV. Liberti* Heer are nearly allied to *JV. Uexuosa* Sternb.

**Neuropteris** ROTUNDIFOLIA.

Brongniart (5, p. 238), in giving specific rank to the form of *Neuropteris* pinnule known as *S. rotundifolia*, expresses doubt as to its specific distinctness from *If. flexuosa* Sternb. Bunbury (7, p. 248), when speaking of this species, says: "I cannot but believe this to be a mere variety of *flexuosa* Sternb., as I have seen on the very same fragments leaflets corresponding with the characters of both."

## N. HETEROPHYLLA.

A close study of the figures and description published by Zeilw (20, p. 261, Pis. 43, 44) of *JV. heterophylla* Brongn. shows that the specimens he figures are portions of large fronds of the *N. flexuosa* Sternb. type, showing its heterophyllous character.

These illustrations (see text-fig. 1, p. 298) have considerable value and interest, as they show pinnae having the characters of *N. heterophylla* Brongn. and *If. flexuosa* Sternb., together with intermediates, all borne on the same rachis. An indication of so clear a character of the actual occurrence of two supposed species types upon the one rachis, and also in association with intermediates, can hardly be set aside.

Such fronds are rarely obtained in large masses, and the opportunity of surveying the whole or a large portion of a whole frond does not often occur, and therefore few comparisons between pinnae in various positions can be obtained. In the case just cited, the lowest pinna in the left-hand corner of the specimen figured (text-fig. 1, p. 298) is of particular interest, as it shows two kinds of lateral pinnae occurring on opposite sides of the same rachis. Only single, large, and simple pinnules are found on the upper side of this, whilst on the lower side small pinnae occur, having the apical pinnule of the same size and shape as the simple pinnules found on the other side.

The late Dr. E. A. N. Arber (1, p. 171) was the first worker to point out this dimorphic character, which he found in a specimen identified by him as *W. qua* Brongn. The great caducity of the pinnules may perhaps be the reason why so few of these dimorphic fronds are found.

Lindley and Hutton (15, p. 183) figured one of these dimorphic pinnae, which they identified as *N. heterophylla* Brongn.

Dr. E. A. K. Arber (2, p. 33) figures a single pinna, and refers it to *W. heterophylla* Brongn. In the light of knowledge gained from a study of a large number of specimens, I identify the pinna as referable to *W. flexuosa* Sternb. The pinnules are certainly more rotund than is the case in normal *W. flexuosa* Sternb. Or "of *N. flexuosa* Sternb. thus approaching the varietal form of *H. Juxmuia* known as *If. rotundifolia* Brongn.

It is of interest to note how many of the same authors who have described and identified *J. Neuropteris* fronds compared them with *If. flexuosa* Sternb.,<sup>48</sup> as this species represented the genus type of the *J. Neuropteris* frond.

NEUROPTHEUS SORETHII ; N. MICROPHYLLA ; N. THYMIFOLIA.

*IT. Sorethii* Brongn., *IT. microphylla* Brongn., and *N. thymifolia* Sternb. are youthful forms of species belonging to the "species-group" of which *N. Jiexuosa* Sternb. is the type and most probably to *N. flexuosa* Sternb. itself. The only differences occurring among these species are those governed by age and position, such as size, compactness of venation, etc. In comparing *N. microphylla* Brongn. with *IT. Jiexuosa* Sternb., Brongniart (5, p. 245) says. "With the exception of the great difference in size, one would consider it to be the same plant." And Schimper (18, vol. i. p. 441) is of the same opinion. He also suggests uniting *IT. Loshii* Brongn., *IT. tenuifolia* Schlofeli. (sp.), and *N. Sorethii* Brongn. with *N. flexuosa* Sternb., as he possessed specimens of these species which appeared to be intermediates.

N. PLICATA.

Dr. Kidston (14, p. 95) placed *N. plicata* Sternb. with *N. flexuosa* Sternb., as he was unable to find any point by which they could be separated, but later (Trans. Hoy. Soc. Edin. vol. xxxv. (1889), pt. 5, p. 313) he decided that the true *N. plicata* Sternb. was not a variety of *IT. Jiexuosa*. Specimens of this species are very rare, and I have not seen one.

N. OVATA.

The description given by Dr. Kidston (10, p. 360) of Hoffmann's species states that "the terminal pinnule in *Neuropteris ovata* Hoffm. is novel\* enlarged as in *N. flexuosa* Sternb. It is usually more or less broadly lanceolate, and at its basal extremity is connected with the uppermost pinnule or pinnules. The pinnules are auricled in a manner similar to those of *N. flexuosa* Sternb., but they do not overlap so much as in the latter-mentioned species. The veins are more arched than in *N. flexuosa* Sternb. and also appear more numerous." All the distinguishing characters, as given by Dr. Kidston, between these two species are such as are entirely dependent on age and position on the rachis. Again, *JS. ovata* Hoffm. differs so slightly from some forms of *N. Loshii* Brongn. that a close relation between the two seems inevitable.

*Revised diagnosis* O/NEUROPTHEUS FLEXUOSA Sternb.

Fronde dimorphic, containing both major and minor pinnules. Minor pinnules varying in size up to 1.5 cm. in length and 1 cm. in width, elongate-oval or oval, occasionally rotund, attached to the axis by a small part of the base. Apical pinnule very large, with the greatest width usually occurring just below the middle of the pinnule. Lateral veins very clear, medium thickness, not much arched, dichotomising two or three times. Median vein clear, running up about three-quarters of the pinnule, then dividing up into smaller veins. Major pinnules large, generally similar in shape and size to the apical pinnules of the minor pinnae. Attached to the rachis by a small part of the base. Venation as in minor pinnules.

*Distribution.*

*N. flexuosa* Sternb. is common throughout the Coal Measures of Great Britain, and also in the Middle Coal Measures, as also are its intermediate forms.

NBDBOPTJBBIS GIGANTEA Sternb.

- 1820  
 1823\* Schlotheim, Die Petrefactenkinde, p. 411.  
*Osmonda gigantea* Sternberg, Essai d'une Exposé géognostico-botanique de la flore du monde primitif, vol. 2, fasc. 1, p. 32, pi. 22.  
 1826. AT Schlotheim, Die Petrefactenkinde, p. 411.  
 1830. Schlotheim, Die Petrefactenkinde, p. 411.  
 1832. Schlotheim, Die Petrefactenkinde, p. 411.  
 1848\* Lindley & Upton, Fossil Flora, vol. i. pi. 52.  
 Sauveur, Végétaux fossiles des terrains houillers de la Belgique (Académie royale des sciences de Belgique), Bruxelles, pl. 33, fig. 1.  
 1848. *Neuropteris flexuosa* Sauveur (non Sternberg), *ibid.* pl. 32, figs. 91, 92.  
 1886. *Neuropteris gigantea* Zeiller, Flore fossile du Bassin houiller de Valenciennes, 258, pl. 42, fig. 1.  
 1892. Potonié, Ueber einige Oaibuufai-ne, iii. Theil, p. 22, text-figs. 1-4, pl. 2, figs. 1-2; pl. 4, figs. 1-4, 2.2 (Jahrb. d. K.-Preuss. Geol. Landesanst., 1891).  
 1892. *Neuropteris Zeilleri* Potonié (5), Ueber einige Carboifarne, iii. Theil, pp. 22, 32, fig. 105.  
 1899. Hoffmann & Ityba (part), Leitpflanzen, p. 64, pl. 9, figs. 4, 4a, 4d.  
 1899. Zeiller, Flore fossile du lias houiller d'Heracle, p. 44, pl. 4.  
 1899. *Neuropteris gigantea* Potonié, Lehrb. d. Pflanzenpal. p. 113, fig. 102.  
 1901. *Neuropteris gigantea* Zeiller, Elements de Paleontologie, p. 105, fig. 79.  
 Kidston, in Proc. Yorks. Geol. & Polytech. Soc. vol. xiv. (1901), pp. 193, 211, 213, pl. 28, fig. 5; pl. 29, fig. 4.

Remarks on synonymy of *N. GIGANTEA* Sternb.

Sternberg's description of *N. gigantea* is very vague in his description of this species published in 1823. He says "it is the largest known form, he proposes to call it *Osmonda gigantea*. Fortunately his figure of the specimen which came from Schatari is clearer than his description. In the same work he figures *Osmonda gigantea* which he states "appears to be a species or variety of *Osmonda gigantea*". This supposed varietal form has, however, characters intermediate between those assigned to *JV. flexuosa* Sternb. and *JV. tenuifolia* Schloth. (sp.).

*N. FLEXUOSA.*

*N. gigantea* Sternb. is confused up with *N. flexuosa* Sternb. by a number of authors. In the presence of the terminal pinnule, it is frequently difficult to distinguish between them. In fact, Bunbury (6, p. 45), in describing some



intermediate forms, expresses doubt as to whether *JV. flexuosa* Sternb. and *N. gigantea* Sternb. are specifically distinct. Brongniart (5, p. 240), noting the resemblance between *N. flexuosa* Sternb. and *JV. gigantea* Sternb. states that the pinnules are longer and narrower in *N. gigantea* Sternb. I do not agree with this statement, as I have seen specimens of *N. flexuosa* Sternb. in which the pinnules show a close approximation in these features to *N. gigantea* Sternb.

#### NEUROPTERIS GRANGERI.

Schimper (18, p. 441) expresses the view that *N. Grangeri* Brongniart is intermediate between *JV. flexuosa* Sternb. and *N. gigantea* Sternb. Brongniart (5, p. 237), whilst separating *N. Grangeri* from *N. gigantea* considers that the differences may be due to the positions which the plant fragments occupied on the one rachis.

#### N. CISTII.

Brongniart is similarly in doubt of the existence of a true specific distinction between his own species *N. Cistii* and *JV. Grangeri*. My own studies have confirmed this view. In some cases pinnules having the characters of *JY. tenuifolia* Schloth. (sp.) occur on pinnae which are undoubtedly specimens of *N. gigantea* Sternb. Pinnules of this character are shown to occur even on the figure of the type-specimens (text-fig. 3).

I have seen several specimens showing both types of pinnule on the same plant. This evidence seems to be conclusive as to the identity of one form with the other.

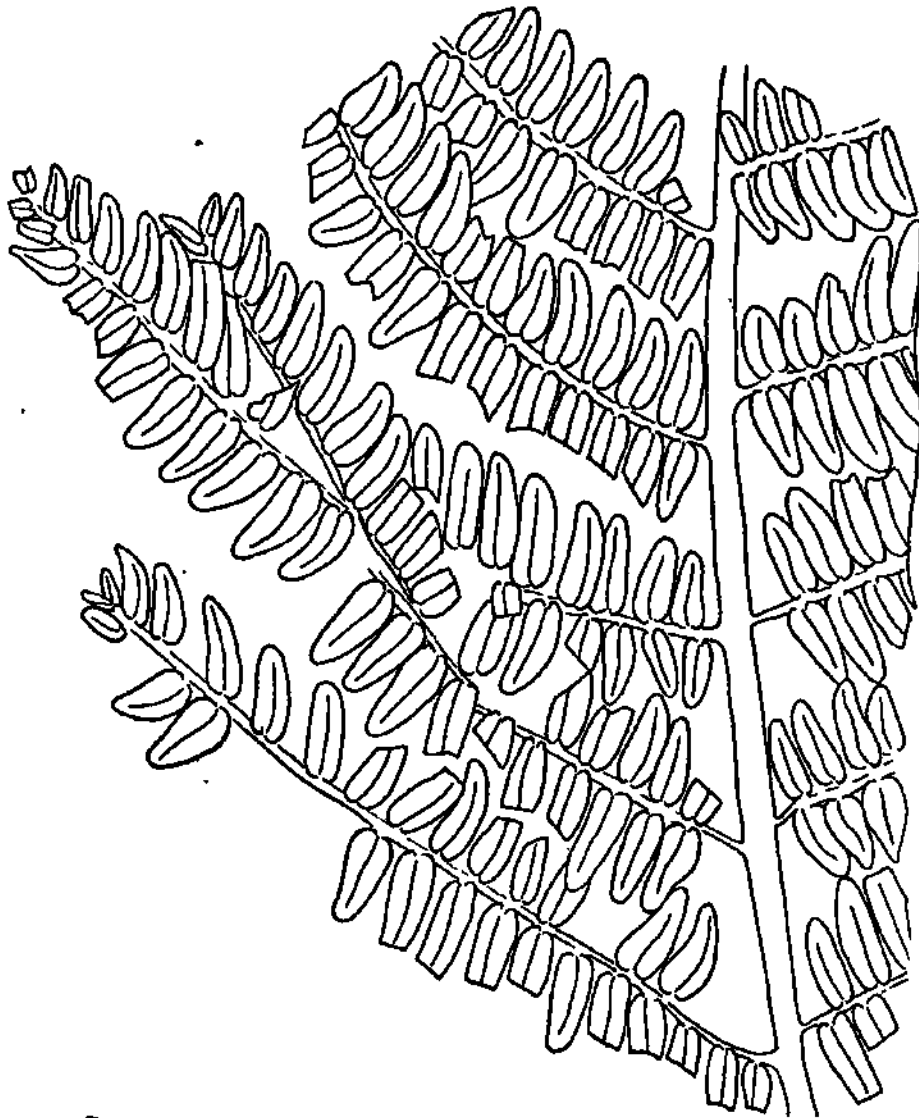
#### *Diagnosis of NEUROPTERIS GIGANTEA Sternl.*

*N. foliis bipinnatis, pinnis patentibus elongatis, pinnulis vix contiguis (nec imbricatis) oblongis obtusis, basi rotundatis (nec dilatato-cordatis) ; nervis tenuissimis approximatis arcuatis dichotomis ; nervo medio vix distincto evanescente.*

Brongniart published this diagnosis of Sternberg's species in 1830 (5, p. 240), as that author gave an illustration only. Zeiller (20, p. 42) gives a very full description of the species, and therefore I include it here :—  
" Fronds very large, tripinnate, secondary rachis 5-12 mm. wide, marked with longitudinal striation, also with irregular punctations corresponding without doubt to scales, and having orbicular or oval pinnules between the secondary pinna, which are contiguous or else overlapping. Primary pinnules 20-30 cm. apart, slightly overlapping, 20-35 cm. wide, and not less than 80-100 cm. long, remaining the same size for a large part of their length\* but becoming smaller towards the top. Secondary pinnae alternate, or sub-opposite, straight or slightly arched, 2-5 cm. apart, contiguous or, what is more usual, overlapping, 25-55 mm. wide, 12-20 mm. long. Narrow, oval,

lanceolate in apex, contracted at the top to an obtuse apex. Pinnules sub-opposite or alternate, sessile, ensily detached, straight, 10-25 mm. long, \*10 mm. wide, contiguous or overlapping. Heart-shaped at the base, margins are finely crenulate, diminishing somewhat in length towards apex of the pinna. Terminal pinnule oval, smaller than the rest.

Fig. 8.



Reduced from figure of type-specimen of *Neuropteris gigantea*.

The pinnules of stacked directly to the rachis are either orbicular, oval, or triangular with rounded angles, 5-15 mm. long, 3-12 mm. wide. Median vein is marked by a slight groove, dividing a little beyond the middle of the pinnule. The pinnules are frequently devoid of a median vein, the veins being out from the point of attachment.

*Distribution.*

*N. gigantea* occurs throughout the British Coal Measures. It is not very common in the Lower Coal Measures, its maximum development being reached in the Transition and Upper Coal-Measure Series.

## NEUROPTERIS TENUIFOLIA Schloth. (sp.).

1820. *Filicites tenuifolius* Schlotlieim, Die Petrefactenkunde, p. 405, pi. 22. tig. 1-  
 1826. *Neuropteris tenuifolia* Sternberg, Flora der Vorwelt, Vers. i. fasc. iv. p. 17 j Vew. \*  
 fasc. v.-vi. p. 72.  
 1828. ————1 Brongniart, Prodrôme, p. 53.  
 1830. ————Brongniart, Histoire des Végétaux fossiles, p. 241, pi. 72. fig. 3.  
 1862. ————Bronn, Lethaja Geognostica, vol. i. pi. 11, p. 110; pi. 7. fig. 4 a, b.  
 1809. ————Schimper, Traité de Paléontologie, p. 438.  
 1886. ————Zeiller, Flore fossile du Bassin houiller de Valenciennes, p. 273, pl. \*  
 fig. 1.  
 1848. *Neuropteris gigantea* Sauveur (non Sternb.), Végétaux fossiles des terrains houillers  
 de la Belgique, pi. 31. tig. 344. "

*Remarks on synonymy of N. TENUIFOLIA Schloth. (sp.).*

## N. GIGANTEA.

Brongniart (5, p. 241) and Schimper (18, vol. i. p. 438) noted the resemblance of *If. tenuifolia* Schloth. (sp.) to *If. gigantea* Sternb., the latter stating that *If. tenuifolia* Schloth. (sp.) is distinguished by its smaller pinnules, which are closer together, and by the distinctly heart-shaped base; also the pinnules are less caducous.

## N. HETEROPHYLLA.

Zeiller (20, p. 275) states that *If. tenuifolia* Schloth. (sp.) greatly resembles *H. heterophylla* Brongn. in many respects, and that many authors have suggested uniting them, seeing in them very near varieties or even forms of one and the same species. Zeiller (20, p. 275) was unable to reconcile himself to this point of view, and gave his reasons why they should not be united. Zeiller's view that these two species should not be united is in my opinion the correct one, and for the same reasons, namely that *N. tenuifolia* Schloth. (sp.) appears to offer in the form of its pinnules and in its nervation perfectly constant characters without transition towards *N. heterophylla* Brongn.

Certain forms of *Neuropteris pinnae* which have a close relationship with *N. tenuifolia* Schloth. (sp.) are included in *N. heterophylla* Brongn.

Zeiller (20, p. 274) gives the impression that he considered all specimens of *N. tenuifolia* Schloth. (sp.) to be of the same size, and that he did not recognize the possibility of smaller and less mature forms. These younger forms have been, I believe, frequently grouped with *N. heterophylla* Brongn.

## N. FLEXUOSA.

The same author also notes a slight resemblance between *If. tenuifolia* Schloth. (sp.) and *If. flexuosa* Sternb., but thinks they can be easily

distinguished. My investigations, both on the published figures of other authors and upon material, seen in collections and in the field, have shown the existence of a series of intermediate forms linking up *JH. tenuifolia* Schloth. (sp.), *N. flexuosa* Sternb., and *N. gigantea* Brongn.

In the specimen (now in the possession of the Bristol Museum) figured on PL. 5. it will be clearly seen that while the uppermost pinnules undoubtedly belong to *N. tenuifolia* Schloth. (sp.), the lower ones have the characters associated with *N. flexuosa* Sternb. In fact, given one of these lateral pinnules separately, it would certainly be identified as *N. flexuosa* Sternb.

*Diagnosis of N. TENUIFOLIA Schloth. (sp.).*

Although Schlotheim is the author of the species, he does not give a diagnosis, evidently considering his figure to be sufficient. Brongniart's diagnosis (5, p. 241), which is as follows, agrees with Schlotheim's figure.

*N. foliis bipinnatis, pinnis elongatis; pinnulis approximate contiguis vel subimbricatis, oblongis, apice attenuatis obtusi, basi cordatis, nervo medio  $\angle$ le notato, apice evanescente; nervulis obliquis, arcuatis,  $\angle$ chotomis, approximatis, tenuissimis; pinnula terminali lanceolata acumata, tanquam neata sublobata, lateralibus triplo longiore.*

*Distribution.*

This species occurs in the Upper, Transition, and Middle Coal Measures, but has not, so far as I am aware, been recorded from the Lower Coal Measures, its maximum is reached in the Upper Coal-Measure Series. It is common in all the British coalfields.

NEUROPTERIS MAOROHYLLA Brongn.

1822. *Neuropteris maorophylla* Brongniart, Histoire des Végétaux fossiles, p. 25, pi. 21.

1869. ——— Schimper, Traité de Paléontologie Végétale, vol. i. p. 434.

1881. ———— 14e ann. Oeuvres de Hotanique Fossile, p. 173. .. 21.

1888.—(Kidston) Proc. Roy. Soc. Edin. vol. x. pt. n. (1888), p. M, pi.

1843. *Neuropteris* Lesquereux, in R. S. Wood's Geology of Pennsylvania, vol. ii. p. 857, pl. 6, figs. 1-4.

**X** ——— Lesquereux, Coal Flora of Pennsylvania, p. 94, pl. 9, figs. 1-6.  
*Neuropteris scheuchzeri* Kidston (non Hoffmann), Catalogue Paléozoic Plants, p. 95.

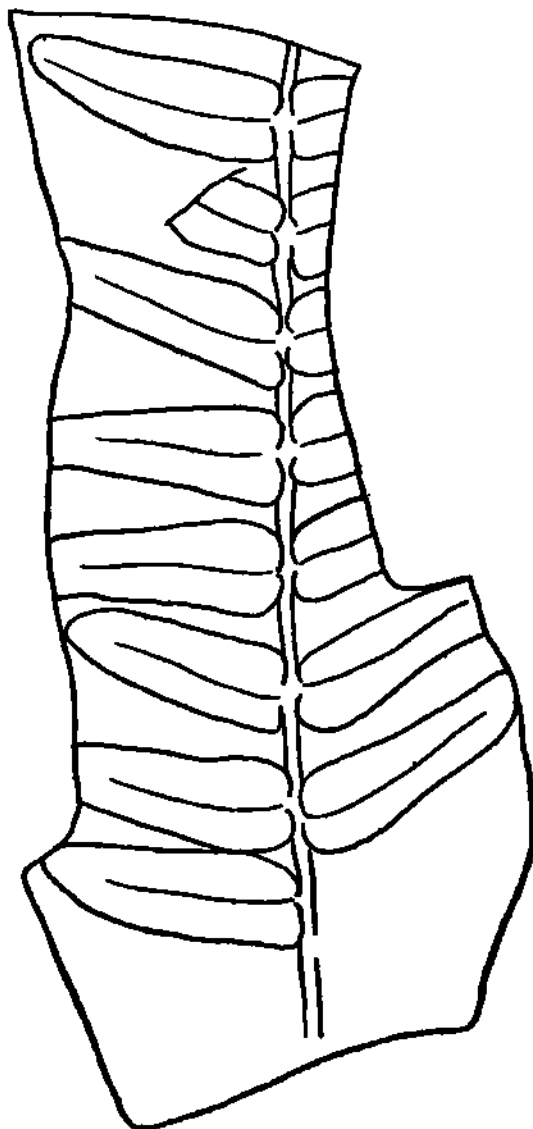
*Remarks on synonymy of S. MACROHYLLA Brongn.*

Most of the older authors, in commenting on this species, remark on its resemblance to the recent fern *Osmunda*, but they differ as to which species of the latter it most resembles. Brongniart compares it to *O. regalis*; whilst Renault and Schimper consider it more closely related to *O. cinnamomea* Willd.

## NEUROPTERIS SCHEUCHZERI.

The pinnules of *N. macrophylla* Brongn. are very caducous (which suggests that they are fully mature), and when found isolated they are difficult at in sight to distinguish from those of *N. Scheuchzeri* Hoffm. A careful examination of the pinnules of the latter species reveals the presence of hairs on the upper surface of the pinnule, a feature shared, so far as is known present, with no other species of *Neuropteris*.

FIG. 4 a.

*Neuropteris macrophylla* Brongn. after Brongniart (reduced).

## N. TENUIFOLIA.

At Crawcrook Clay Pit, Co. Durham, I have seen numerous specimen intermediate in character between the smaller forms of *N. macrophylla* Brongn\* and the larger forms of *N. tenuifolia* Schloth. (sp.). These link up *N. macrophylla* Brongn. with the four species previously described (*N. flexnosa* Sternb., *N. gigantea* Sternh., *N. ovata* Hoffm., and *N. tenuifolia* Schloth., sp.).

NEUROPTERIS AURIOULATA.

Certain forms of *N. macro-pjiylla* Brongn. are not unlike *N. auriculata* Brongn., and there is good reason to believe that they are intermediate forms connecting the two species.

FIG. 4 b.

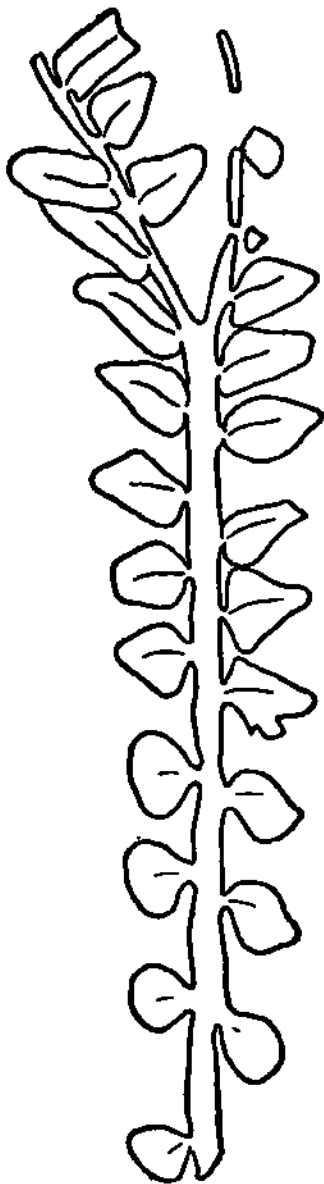
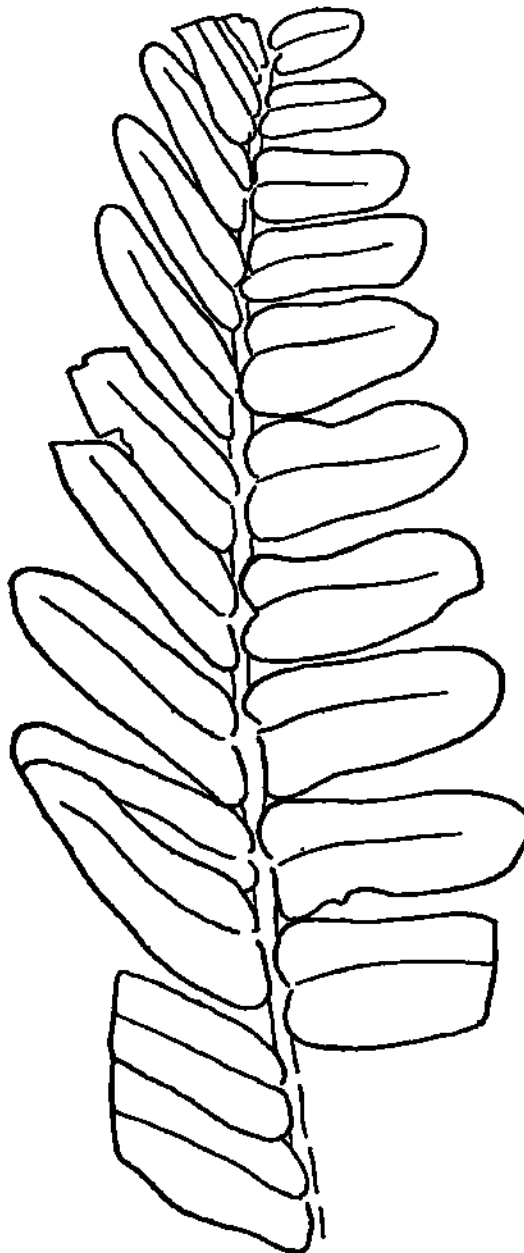


FIG. 4 c.



*Neuropteris macrophylla* Brongn., both after Kidston (reduced).

*Diagnosis of S. MACROPHYLLA* Brongn.

*W. pinnatis* pinnatis, pinnulis distantibus oblongis, obtusis, *I. J. Ualibus* cordatis, angulo inferiore paulatim extenso; nervo medio valde *st. to*; nervulis dichotomis, e nervo medio nascentibus, arcuatis. *he* *from* *TM* very large, with the pinnae dividing by a series of *bil. recations.* The pinnules, which alternate on the rachis, are of varying

size and shape, being triangular, lanceolate-acute, oblong-obtuse, and eye-pteroid. As in most species of *Neuropteris*, the midrib is distinct in the greater part of the pinnule, but breaks up by a series of dichotomies in numerous fine veins, which are arched and usually forked four times.

*Distribution.*

This species occurs in the Upper, Transition, and Middle Coal Measures, but has not yet been recorded from the Lower Series. The maximum development occurs in the Upper Oonl Measures, where it is parfcicnla"? common. It is recorded from five of the seven coalfields of England.

**NEUROPTERIS HETEUOPHTLLA Brongn.**

1822. *FUiritea (Neuropteris) heterophyllns* Brongnimrt, Classification des Ve'gStanx fossils pp. 33, 89, pi. 11. figs. 6 a, (\b.
1828. *Neuropteris Jteterophylla* Brongniart, Prodr6me, p. 53. Td., Ilistoire des V<SgeW\* fossiles, p. 243, pi. 71; pi. 72. fig. 2.
1833. *Neuroptem Brongniartm* Steruberg, Essai d'nn Exposed geognostico-botanique de flore du moiule primitif, vol. ii. fasc. v., VT. p. 72.
1830. *Neuropteris Loshii* Brongniart, Ilistoire des Ve\*g<Staux fossiles, p. 242, pi. 72. fig- 1 pi. 73.
1830. *G/ekhenites neuropteroides* Goeppert, Systema filicum fossilium, p. 186, pis- 4<sup>th</sup>.
1838. *Filicites Goepperti* Presl, in Sternberg, Essjiid'un Expos6 geognostico-botanique <e la flore du monde primitif, "vol. ii. fasc. VII.-VIII. p. 175.
- 18G2. *Otlontopteris oblongifolia* Roemer, Palseontographica, vol. ix. p. 31, pi. 7. fig. !.
1868. *OiUmtopteris hritanica* Roehl, Palaeontographica, vol. xviii. p. 41 (pars), pi. 20. fig- 4,
- 18G8. *Odontopteris obtusihba* Roehl, Palrcontographica, vol. xviii. p. 42, pi. 10. figs- 12~\* 5,

*Remarks on synonymy of N. HETEROPHYLLA Brongn.*

After examining a large number of specimens identified by many vario<sup>5</sup> workers as *N. heterophylla* Brongn., I am doubtful whether this can<sup>1</sup> be considered as a valid species, or whether many specimens identified und<sup>1</sup> this specific name will not, in most cases, prove to be young or varietal form,<sup>9</sup> of other well-known species.

**N. LOSHII.**

As I have previously stated in dealing with *N. flexuosa* Sternb., I<sup>hs1V</sup> become convinced, after careful study of much material, that the form known as *N. Loshii* Brongn. and included by most authors as a synonym of JV. *heterophylla* Brongn. is really an immature condition of *N. flexuosa* Sternb.

Again, a few of the forms included in JV. *heterophylla* Brongn. are dimorphic a character which is not confined to this species. Arber (1, p. 171) h<sup>1S</sup> shown that the species *N. obliqua* Brongn. is also dimorphic, having la<sup>r8</sup> msijor pinnules and smaller bipinnate minor pinnules, and that both frequently occurred on the same pinnae.

**NEUROPTERIS FLEXUOSA.**

I have figured *N. flexuosa* Brongniart (5, pi. 71) many of the lateral pinnae  
 ex-<sup>^</sup>ternally associated with *N. flexuosa* Sternb. Brongniart's  
 two species of the existence of intermediate forms linking the  
 species *heterophylla* Brongn. and *N. flexuosa* Sternb.

**N. TENUIFOLIA.**

Schimper (1846, p. 438) referring to *N. heterophylla* Brongn. says,  
 "This species does not appear to be distinct from *N. tenuifolia* Schloth."  
 Brongniart had already expressed doubts when he said, "It is possible, how-  
 ever, that these two plants are only varieties of the same species." "I feel  
 tempted to go so far as to say, not to go even further and unite with *N. tenuifolia*  
 Brongn., *N. tenuifolia* Schloth., and *JV. Soretii* Brongn., as I possess specimens  
 of these different plants which appear to offer passages between each other."  
 I have found similar intermediates.

The specimen figured by Zeiller (20, pi. 43) under the designation  
*N. heterophylla* Brongn. is evidently the apical portion of a large frond  
 of *N. flexuosa* Sternb. (see text-fig. 1, p. 298). Two forms of pinnules  
 in the frond. Those about the middle of the specimen are very similar  
 to those of *N. tenuifolia* Schloth., but where the pinnae become  
 compound we associate with *N. flexuosa*  
 Sternb.

The portion of frond on plate (Zeiller, 20, p. 44) apparently  
 grew down on the rachis. In one part of it the dimorphic character  
 is clearly known for one side of the rachis bears single pinnules of the form  
 of *N. tenuifolia* Schloth., whilst the other has pinnules similar to those  
 of *N. flexuosa* Sternb.

The diverse characters of the many specimens included in the species  
*N. heterophylla* Brongn. and the laxity allowed by the original diagnosis has  
 caused it to become a dumping ground for all doubtful species of  
 pinnae.

**Diagnosis of N. HETEROPHYLLA Brongn.**

foliis tripinnatis, quandoque e basi bifurcatis, pinnis alternis  
 superioribus inferioribus brevissimis; pinnulis formâ diversis  
 superioribus inferioribus oblongis subovatis; intermediarum ovatis,  
 latioribus rotundis minimis paucioribus; terminalibus oblongo-lanceo-  
 lis, lateralibus multo longioribus; omnibus basi cordatis,  
 nervis arcuatis tenuissimis.

**Distribution.**

From the Coal-Measure Series and in all the coalfields of Great  
 Britain.

LINN



NEUROPTERIS RARINERVIS Bunbury.

- 1847. *Neuropteris rarinervis* Bunbury, Quart. Journ. Geol. Soc. vol. iii. pp. 425, 438, pi. 2tZ.
- 1870. *Neuroptn.* <sup>corf^</sup>, LeSquereux) Qeol ^ . . rf Illinois, ^ . y 1 . p.38?> pl. 8. <sub>figs. 7-8.</sub>
- 1876. *Neuroptn.* <sup>att^ata</sup> Boulay (non Lindl ey & n^utton), Ten. ^ da Nord de l>
- 1878 V <sup>F T F F</sup> <sub>P 30 74 pl. 4</sub> \* \* \* L
- 1878. <sup>tfwj p JJ</sup> ^ > / % « Zeffler (<< m Brongniart), Expl. carte g6ol. France, vol. i\*  
p. 49 (part).

Remar^ om ^ «out V my aff N\* KARRINBBWISS i? , m & M ^ .

It is vnth doubt that I include this species in the species-gronp *N. flexuosa*. I have been mnable to find any species of *JYeuropteri\** with which *N. rarinervis* B<sup>TM</sup> 7 S t0 have «7 ^uo affinity, unless it be with *KM\*\*'* Sternb<sup>i</sup> which it resembles in the form of its pinn\* and pinnules. *N. ran-* Bunb<sup>i</sup> ET ffl 7, r6 T. inS for tho time being S an Elated species, having no known affin.hesw.th any of the present species-groups.

N. FLEXUOSA.

In general form of the frond and in the outline of the pinnules it much resembles *N. flexuosa* Sternb., and upon a hasty examination it might 1\* mistaken for that species, from which it differs in its venation. The veins of ^ . m n ^ r m Bunbury, are farther apart than in any other member of the genus' and though arched in the manner characteristic of the genus, «re scarcely ever more than twice forked, indeed in many of the smaller pinnules only once. The comparatively few thick veins ought to render it an easy species to dis<sup>t</sup>.ngmsh. It is also the only species of *Muropieris* in which I h f d the chaTcteT n UmbGr of V6inS Per centimetro t0 be r < \* < > ' to a « a « liag n09tio

Diagnosis o/N. BABINBBVIS Bunbury.

The frond is bipinnate, the main stalk striated and rather slender in proportion; the pinna, partly opposite and partly alternate, narrow and almost linear in their general outline. Pinnules closely set, but not usually over! and somewhat dilated at the base, where they «are more or less auricled j they IZ^r^u- aPPear t0 lmVS b6en of a firm insistence ; their surface is ZL V 27 ^ m g 6 r al the larg est and > ost elongated. The veins arc one apTh ^ T T ^ a i T mdy sMad L a b w d te

Distribution.

This species is Series and in most of the ^ coal fild « Kup u is never common. n ^ U P P or Tr mition, and Middl « Coal-Measure

NEUROPTERIS SCHEUCHZERI Hoffm.

1820. *Neuropteris Scheuchzeri* Ploffmann, in Keferstein's Teutschland geognostisch-geologisch dargestellt, vol. iv. p. 156, pi. 1 b, figs. 1-4.
1840. *Mwropteris angmtifolia* Brongniart, ilistoire dea VSgétaux fossiles, p. 231, pi. 64. figs. 3-4.
1840. *Neuropteris acutifolia* Brongniart, Ilistoire des Ve'gétaux fossiles, p. 231, pi. 64. figs. 6-7.
1832. *Neuropteris cordata* Liidley & Tlutton (non Brongn.), Fossil Flora, vol. i. pi. 41.
1858. *Neuropteris hirsuta* Lesquereux, in Rogers, Geol. Pennsylv. vol. ii. p. 857, pi. 3.
1899. *Scheuchzeri* Roomer, Paleontographica, vol. ix. p. 30, pi. 9. fig. 1.
1896. *Neuropteris Scheuchzeri* Zeiller, Flore fossile du Bassin Louiller de Valenciennes, p. 41. 1-3.
1892. ———— Kidston, Ve'gétaux Ilouillers dans le Hainaut Beige, p. 80.

Remarks on synonymy of *N. SCHEUCHZERI Hoffm.*

It is with some doubt that I suggest the placing of *N. Scheuchzeri* Hoffm. in the species-group *N. flexuosa*. At first sight the pinnules of this species, especially when found isolated (which is often the case), seem to be a large form of *N. tenuifolia* Schloth. or *If. macrophylla* Brongn. Careful examination will reveal, however, the presence of fine hairs, which occasionally give the appearance of anastomosing veins covering the surface of the pinnule. This is the only known species of *Neuropteris* which is hairy. The frequent presence of a small basal pinnule on the lower side of the large pinnule is bother distinguishing feature.

All the specimens of *If. Scheuchzeri* Hoffm. that I have seen have had the appearance of being fully mature. The presence of hairs may be a condition of maturity, and the young fronds, being destitute of such hairs are yet recognized. In all probability they must be looked for amongst the many samples referred to the species-group *JV. flexuosa*. Conversely, it may be that *N. Scheuchzeri* Hoffm. is not hairless in its immature stages, but that the hairs, being very fine and delicate, were lost during fossilisation. This, I think, is the more likely.

Diagnosis of *N. SCHEUCHZEJII Hoffm.*

Frond very large, tripinnate. Secondary rachis 10-20 mm. wide, marked, rachis of the third order, with fine regular longitudinal striae, and wing, on the rachis between the secondary pinnse, pinnules like those on Pinua. Secondary pinnae alternate or sub-opposite, 6-16 cm. apart, overlapping a little on each other, 6-15 cm. wide, 20-60 cm. long, linear-lanceolate or oval-lanceolate in shape, sometimes slightly restricted at the base, being the same width over nearly the whole of their extent and then tapering to a point. Pinnules alternate or sub-opposite, nearly sessile, easily curved, straight or curved back like a scythe, 2-10 cm. long, 8-25 mm. touching a little along their margins or else clearly separated, tapering

to a sharp point at the apex, rounded at the base of the lower side or often enlarged into a slightly projecting ear-shaped structure, truncated obliquely on the upper side and flanked by a small orbicular or oval pinnule rounded at the top, 5-12 mm. wide and 2-8 mm. long. Towards the top of the secondary pinnae this small basal pinnule is united to the large pinnule of which the base is then cordiform.

Terminal pinnule of the secondary pinns is a little longer than preceding ones, but equally pointed at the apex. The pinnules attached directly on the secondary rachis are generally a little shorter than the others, always have two small independent pinnules at the base, one above and one below, both rounded or obtusely pointed at the apex, and being nearly 15 mm. long, sometimes only the upper small pinnule remains independent, as on the secondary pinnae, and the other completely united, simply forms a lobe at the base of the large pinnule.

Median vein clear, dividing a little beyond the middle of the pinnule. Secondary veins arise at a very sharp angle, then gradually arched, dividing several times into fine compact veinlets. Lower surface of the pinnule, large or small, bristling with stiff, scattered hairs, 1.5-2 mm. or nearly 3 mm. long, lying almost parallel to the median vein. (Zsiller, p. 252.)

#### Distribution.

*If. Scheuchzeri* Hoffm. is found in the Upper, Transition, and Middle Coal Measures, being particularly common in the Upper Coal Measures.

#### Conclusions drawn from a critical study of the Species-group N. FLEXUOSA.

A close study, extending over four years, on some hundreds of *Neuropteris* pinnules, has led me to the conclusion that the five species, *IT. flexuosa* Steiner, *N. ovata* Hoffm., *IT. gigantea* Sternb., *IT. tenuifolia* Schloth. (sp.) and *N. macrophylla* Brongn., are closely linked to each other by a series of intermediates, and that they are more sharply defined from all other species. The shape of the pinnule, and the size, form, and venation of the pinnules of specimens identified as belonging to one or other of these five species undoubtedly show that there is some connection between these species.

The general outline of the pinnae shows a great similarity throughout the five species. The largest pinnules are found at the base of the pinna, and their size gradually diminishes as they are traced towards the apex, where they may or may not end in a terminal pinnule. This terminal pinnule is usually larger and of a slightly different shape from the lateral pinnules, having its greatest width at the base rather than nearer the middle, as in the lateral pinnae. The lateral pinnae are, with one exception—*IT. rotundifolia* Brongn.—longer than they are broad. The pinnules of *If. tenuifolia* Schloth. are about the only ones which afford comparatively little difficulty to identify when found isolated, while those of *N. gigantea* Sternb. and *IT. flexuosa* Sternb.

are frequently extremely difficult to separate. In all the species the venation is similar, both in the relative thickness and in the spacing of the veins, and for this reason the number of veins per centimetre can possess no diagnostic value.

*N. flexuosa* Sternb. is the species around which the other four species may be grouped. Typically the species is characterized by a much enlarged terminal pinnule roughly triangular in outline, while the lateral pinnules are longer than they are broad, being in the ratio of 2 : 1. The veins in all the pinnules are moderately fine and fairly close together, the number of veins per centimetre of margin varying between 25-30 according to the age of the pinnule, and the position of the marked centimetre on the margin, whether near the apex or base of the pinnule. The usual number of veins to be found coming to the margin in the middle of a mature leaf is about 35, but it is not a number to be relied on for identification purposes. The veins usually fork twice after leaving their point of origin. In no case does the midrib tend to the apex of the pinnule, but generally breaks up by a series of bifurcations. Between the typical form and the species *X. gigantea* Sternb. occur numerous intermediate forms, which by their varying characters connect *S. flexuosa* Sternb. and *N. gigantea* Sternb. together. In view of the enlarged terminal pinnule of *S. flexuosa* Sternb. it is frequently difficult to distinguish this species from *X. gigantea* Sternb., as the characters of the lateral pinnules are so alike.

*N. ovata* Hoffm. can hardly be regarded as an intermediate species, but rather as an immature condition of *N. flexuosa* Sternb.

Specimens of *N. flexuosa* Sternb. are frequently found in which the terminal pinnule, whilst retaining its characteristic shape, does not become much larger than the lateral pinnules, and where the rounded apex gradually becomes more acute. These examples are intermediates between *X. flexuosa* Sternb. and *N. tenuifolia* Schloth. Where several pinnae are found in a single connection, it will frequently be seen that some pinnules retain more of the characters of *X. flexuosa* Sternb. than do the remainder.

*X. gigantea* Sternb. has some relation to *X. flexuosa* Sternb. and *X. tenuifolia* Schloth. Although the greatest number of specimens agree with the type, others frequently occur having affinities either to *X. flexuosa* Sternb. or *N. tenuifolia* Schloth. (sp.)

The pinnules of *N. tenuifolia* Schloth. often bear a close resemblance to the smaller pinnules of *S. macrophylla* Brongn., and these form the link between the two species. Certain of the specimens now designated as *S. macrophylla* Brongn. can be designated as connecting-links between the present group and the two other species-groups with which

181. U deal later.

From materials I have collected, I have been able to select a series of specimens which exhibit the relationship existing between all the species in the species-group *N. flexuosa* (see Pl. 6). The series includes specimens which are typical of the following species:—*JV. flexuosa* Sternb., *N. gigantea* Sternb., *N. tenuifolia* Schloth. (sp.), and *JV. macrophylla* Brongn., and also a number of intermediate forms linking the species to each other. The relationships are so well established by these examples that it would seem justifiable to conclude that the four species have been founded upon portions of fronds taken from different parts of the same plant. I am of the opinion that the differences which are found to occur in these apparent "species" are such as can be accounted for by the position occupied on the frond or by a difference in age.

A frond belonging to the species-group *JV. flexuosa* may, I think, either *JV. tenuifolia* Schloth. at its apex, and on its becoming pinnate, break up into pinnae having the characters of *JV. flexuosa* Sternb., or, on the other hand, the apical portion may be of the *JV. flexuosa* Sternb. type while the lower pinnules may have the characters of *JV. tenuifolia* Schloth. The first type belonged to pinnae of the primary order and possibly secondary as well, if the frond were tripinnate, while the other pinnae were of the second type.

The reason for such a detailed study of this species-group is that most of its members are common throughout the coalfields of Britain, and therefore a far greater amount of material has been available for examination.

#### Characters of Species-group *N. FLEXUOSA*.

The pinnae have the larger pinnules at the base of the rachis, while the remaining pinnules gradually decrease in size as they approach the apex, which is usually terminated by the largest pinnule. This apical pinnule when present, is of a characteristic shape, being roughly triangular, This type of apical pinnule is found only on specimens belonging to this species-group. The lateral pinnae are either very shortly stalked or else attached to a small portion of the base; in shape they are longer than broad, with the apex varying from round to acute. The veins are moderately fine and stand close together, arising from a mid-rib which extends about two-thirds of the way up the lamina; they usually fork twice after leaving their point of origin.

#### 4 B. Species-group *N. OBLIQUA*.

Synonymy of *JV. obliqua* Brongn. See Arber, Journ. Linn. Soc, Bot. vol. xlvi. (1922) p. 207.

#### Remarks on synonymy of *N. OBLIQUA* Brongn.

The late Dr. E. A. Newell Arber gave so able and concise a statement of the relationships existing between *JV. obliqua* Brongn., *N. callosa* Lesq. and *JV. impar* Weiss (1, p. 201) that nothing more need be added. He recognized the dimorphic character of *Neuropteris* fronds, and after careful

Arch came to the conclusion that *JV. acuminata* Schloth. sp. and *N. imbricata* Weiss were both major pinnules belonging to *N. obliqua* Brongn. As he pointed out, examples of what is probably a closely-allied species, namely *JV. callosa* Lesq., have frequently been wrongly identified as *N. obliqua* Brongn. These two species, like those in the previously-mentioned species-group, appear to be connected by a series of intermediates.

Unfortunately the members of this species-group are comparatively rare, which renders it difficult to obtain good material.

A specimen illustrated on pi. 183 of Lindley & Hutton's \* Fossil Flora, and identified by them as *N. Jieterophylla*, is a specimen of *N. obliqua* Brongn., showing both major and minor pinnules. This is another instance of the totally different types which have been grouped together as *heterophylla* Brongn.

#### Diagnosis of *N. OBLIQUA* Brongn.

The following description is that given by Arber (1, p. 211):—"Fronde dichotomous, composed entirely of minor or of major pinnules, or containing pinnae of both types. Minor pinnules small, up to 2 cm. long and nearly 1 cm. broad, often considerably smaller, elongately oval or elongately triangular, parallel-sided, attached to the axis by the whole base or, in the ladder types, only by a part of the base. Apical pinnule very large or long and narrow. Lateral nerves very little arched, sinuous, each dichotomising 2-3 times, markedly distant from one another in centre of leaf. Major pinnules very variable in size and shape, even in the same pinna, lanceolate (up to 5x2.5 cm.), ovate lanceolate (up to 3-5x2.5 cm.), sometimes very broad and unsymmetrical, attached to the rachis by a very small part of the base, which, however, is sufficiently broad to allow of the origin of some of the basal veins directly from the rachis. The lanceolate pinnules are frequently lobed or have a cyclopteroid-like pinnules attachment and a more radiating nervation, partly directly from the rachis. The lateral nerves are more frequently dichotomised than in the minor pinnules, but possess a similar inclination and are also sinuous in their course."

#### Distribution.

*N. obliqua* is found in the Middle and Lower Coal Measures, but is here very common.

#### NEUROPTERIS CALLOSA Lesq.

1879-80. *Neuropteris callosa* Lesquereux, Geol. Survey Pennsylvania, p. 115, pi. 16.

1909. *Neuropteris callosa* (figs. 1-4) (figs. 5-8).

1911. *Pteris obliqua* Arber, in Quart. Journ. Geol. Soc. vol. Ixv. p. 20, pi. 1. fig. 3.

— Kidston & Jongmans, Arch. Néerl. Sci. Exact, et Nat. ser. 3 B vol. i. p. 25, pi. (unnumbered), fig. 3.

*Remarks on synonymy of N. CALLOSA Lesq.*

Although I quite agree with Dr. Arber in his statement that *N. obliqua* Brongn. and *N. callosa* Lesq. are distinct species, I think that some specimens now otherwise difficult to identify will prove to be intermediate between the two species.

Arber (1, p. 215) suggests a possible relationship between *N. callosa* Lesq. > *N. tenuifolia* Schloth., and *N. heterophylla* Brongn. If this suggestion is correct, and from my researches I think it is, then the two species-groups of *N. flexuosa* and *N. obliqua* will be connected with each other by intermediates in the same manner as are the individual species within species-groups.

*Diagnosis of NEUROPTERIS CALLOSA Lesq.*

Fronde large, tri- or ? quadripinnate. Penultimate pinnae broad, often, but not always, with broad axis; ultimate pinnae lanceolate, axis very slender. Pinnules typically Neuropteroid, inserted by a very small part of the base, or oval or elongately oval, varying much in size from 4 mm. up to 20 mm. more in length, entire, broadly rounded at the apex, markedly cordate, almost eared, at the base, closely set on the axis, and frequently overlap one another. Pinnules markedly caducous. Nervation clearly marked, but nerves fine, all nearly equally strong and equally placed. Lateral nerves all arising from the median nerve, not crowded, somewhat arched, flexuous in their course, dichotomising one to three times. Lamina between veins frequently punctate. Terminal pinnule rather small, elongately lanceolate. (Arber, *op. cit.* i. p. 214.)

*Distribution.*

*N. callosa* Lesq. is found in several of the British coalfields on the horizon of the Transition and Middle Coal Measures

## NEUROPTERIS SCHLEHANI Stur.

1868. *Neuropteris tenuifolia* Iloehl (*non* Sternb.), Palaeontographica, vol. xviii. p. pi. 20. fig. 6.
1877. *Neuropteris schlehani* Stur, Culm Flora, ii, p. 289, pi. 28. tigs. 7,8. Weisk., A Steink. p. 15, pi. 15. fig. 92.
1877. *Neuropteris dluhoschi* Stur, Culm Flora, ii, p. 289, pi. 28. fig. 9.
1879. *Neuropteris elrodi* Lesquereux, Atlas to the Coal Flora, p. 3, pi. 13, fig. 4. Lesquereux, Coal Flora, p. 107; iii. p. 735, pi. 96. figs. 1-2.
1881. *Neuropteris gigantea* Achepohl (*won* Sternb.), Niederrh.-Westfal. Steinkobl. p. pi. 16. fig. 2.
1886. *Neuropteris schlehani* Zeiller, Flore fossile du Bassin houiller de Valenciennes p. 280.

*Remarks on synonymy of N. SCHLEHANI Stur.*

N. TENUIFOLIA and N. OBLIQUA.

The general character of the venation and the shape of the pinnules of the

apical portion of the primary pinna bears a close resemblance to the forms of #. tenuifolia^ot, At the same time the forms of #. Monulob on the secondary pinna suggest affinities with the species-group If. ohliqua, particularly with U. under of #. a6<3<a Brongn. Thus it would appear that the species derivation might be a connecting-link between these two species-groups.

Diagnosis of N. SCHLKHANI Star.

Fronds of great size, at least tripinnate. Secondary rachis marked by fine irregular stations. Primary pinna straight, being 40 cm. long, with a width of 12-20 cm., lanceolate, the same size for two-thirds or three-quarters of their length. Acting to a pointed apex, bipinnate for their greater part at their extremity. Uppermost primary pinna probably

Secondary pinnae alternate or sub-opposite, 12-25 mm. long, 8-30 mm. wide, linear-lanceolate or narrowly ovate, margin, nearly parallel, sometimes slightly curved to a point at the apex, simply pinnate or replaced by large lobed Primary pinna by large, simple pinnules; the base, or else entire, linear, tapering to an obtuse

long, 2-6 mm. wide. Haftly arched, rounded at

Pinnules alternate or sub-opposite, narrow or each margin, contiguous or slightly separated from size very variable according to the position they occupy, 2-6 mm. wide, sessile or with short stalks, attached to the ends of the pinna, where they are divided in shape. The pinnule of the secondary pinna longer than those preceding it, the apex to an obtuse or obtusely-pointed apex.

Median vein clear, marked on the upper side by a very strong and slightly raised, arising at a right angle dichotomising 2-3 times into fine veins, which are almost at right angles. (Zeiller, 20, p. 280.)

Distribution.

Seldehani is found in the Transition and Middle Wales is recorded from these horizons in the Kaustoc fields. I do not know of the species being recorded from any other horizon or locality.



## NEUOPTERIS RECTINERVIS Kidston.

1887. *Neuropteris rectinervis* Kidston, in Trans. Roy. Soc. Edin. vol. xxxv. (1887) P<sup>t</sup> v.  
p. 314.

*Remarks on N. RECTINERVIS Kidston.*

## N. {SCHLEHANI.

In both this species and *N. Schlehani* Stur the venation is character<sup>ed</sup> by the very wide angle most of the lateral veins make with the margin<sup>l</sup> of the pinnule. In *N. rectinervis* Kidston the angle is usually slightly wi<sup>der</sup> than in *N. Schlehani* Stur, being almost a right angle (in this character<sup>th</sup> venation resembles that found in the genus *Alethopteris*). In both iV. *Rectinervis* Kidston and *If. Schlehani* Stur the mid-rib is very distinct, a<sup>nd</sup> extends almost to the apex of the pinnule, while the lateral pinnules are<sup>oval</sup> or oblong. In *N. Schlehani* Stur the terminal pinnule is usually long<sup>er</sup> than that found in *If. rectinervis* Kidston. My observations have led me to conclude that there is a fairly close relationship between the two sp<sup>eci</sup>es. I am aware of the fact that *N. rectinervis* Kidston is regarded as a L<sup>ower</sup> Ooijl-Moasnre form, while i<sup>T</sup>. *Schlehani* Stur is recorded from the Mi<sup>ddle</sup> and Transition Series. This fact does not however, I thi<sup>nk</sup>, preven<sup>t</sup> a relationship existing between them, but rather suggests that the new<sup>er</sup> form may have evolved from the older form of the Lower Coal Measures.

*Diagnosis of N. RECTINERVIS Kidston*

Pinnules sessile, alternate oval or oblong, blunt, approximate or slig<sup>htly</sup> separated; margin entire and free from plications. Mid-rib very dis<sup>tinct</sup> and extending almost to the apex. Lateral veins numerous, distinct, fr<sup>om</sup> springing from the mid-rib with a gentle curve and then running the grea<sup>ter</sup> part of their course almost at right angles to the margin of the pinn<sup>ule</sup> usually once, but occasionally twice, divided. Terminal lobe long.

*Distribution.*

Middle Coal Measures of Uadstock, and Northumberland and Durluun.

*Conclusions drawn from a critical study of the Species-group N. OBLIQUA.*

I include *N. Schlehani* Stur and *JY. rectinervis* Kidston in the sp<sup>eci</sup>es-group *N. obliqua*, but with some doubt. In many characters, chiefly<sup>ly</sup> shape and general outline of the pinnules, *N. Schlehani* Stur resembles some of the minor pinnules of *N. obliqua* Brongn., but at the same time<sup>ly</sup> venation and outline of some of the pinnules also suggest affinities wit<sup>h</sup> iV. *tenuifolia* Schloth., a species included in the species-group *Jf. Jtexuosa*. It would almost seem, therefore, that in the species *JV. Schlehani* Stur we have a form which is an intermediate or connecting-link between the two species-groups. These remarks also apply to the species *If. rectinervis* Kidston.

A characteristic feature of the pinuse placed in this species-group is the tendency of the apical pinnule to become decurrent on the rachis, while

any of the lateral pinnules are attached by a portion of their base, through which veins having their origin in the rachis, pass into the pinnule. This character of the lateral veins is one shared by members of the next species-group P. There is, in fact, a close relationship existing between the members of the species-group *N. obliqua* and those of the species-group *N. auriculata*. In shape, size, and venation some of the major pinnules of *N. Miyua* Jirongn. are very similar to those identified as *N. auriculata* Brougn., and it is these pinnules which form the chief connecting-link.

*Characters of Species-group N. OBLIQUA.*

The pinnules are characterized by comparatively long and narrow terminal pinnules, which have a tendency to become decurrent on the rachis. The lateral pinnules of the "major-pinnule" type are large and not unlike some of those found on specimens belonging to the species-group *If. flejuosa*. Those of the "minor-pinnule" type are small and have a rounded apex. Both kinds of pinnules may be attached either by short foot-stalks or else by a portion of the base; in the latter case some of them have their Oligite, in the former. The mid-rib is clearly marked and extends almost to the apex of the pinnule. Like the apical pinnule, the lateral pinnules show a tendency to become decurrent. The lateral veins are numerous and fork two or three

40. Species-group N. AURICULATA.

*Neuropteris auriculata* Brongn.

1809 *Neuropteris auriculata* Brongniart, Histoire des Végétaux fossiles, p. 240, pi. 6.

1880 ——— Schimper, Traité de Paléontologie Végétale, vol. i. p. 443.

1 ——— Zeiller, Végétaux fossiles du terrain houiller de la France, p. 52.

*Remarks on synonymy of N. AURICULATA Brongn.*

The large-leaved form of *Neuropteris* pinnule is easily distinguished from some of the species forming the two other species-groups. The almost absent definite median vein appears to be of the same nature as in any other species, except perhaps certain large forms of *U. macrophylla* Brongn., which appear to be connecting-links between the two species-groups.

*Diagnosis of N. AURICULATA Brongn.*

Pinnae alternate, pinnae alternate, rachis broad, with cyclopteroid pinnules large (up to 4.5 x 2.5 cm) frequently attached by broad portion of the base through which the veins pass from their point of origin on the rachis. A broad, rounded, margins more or less parallel. Veins fine and compact, median vein almost or entirely absent.

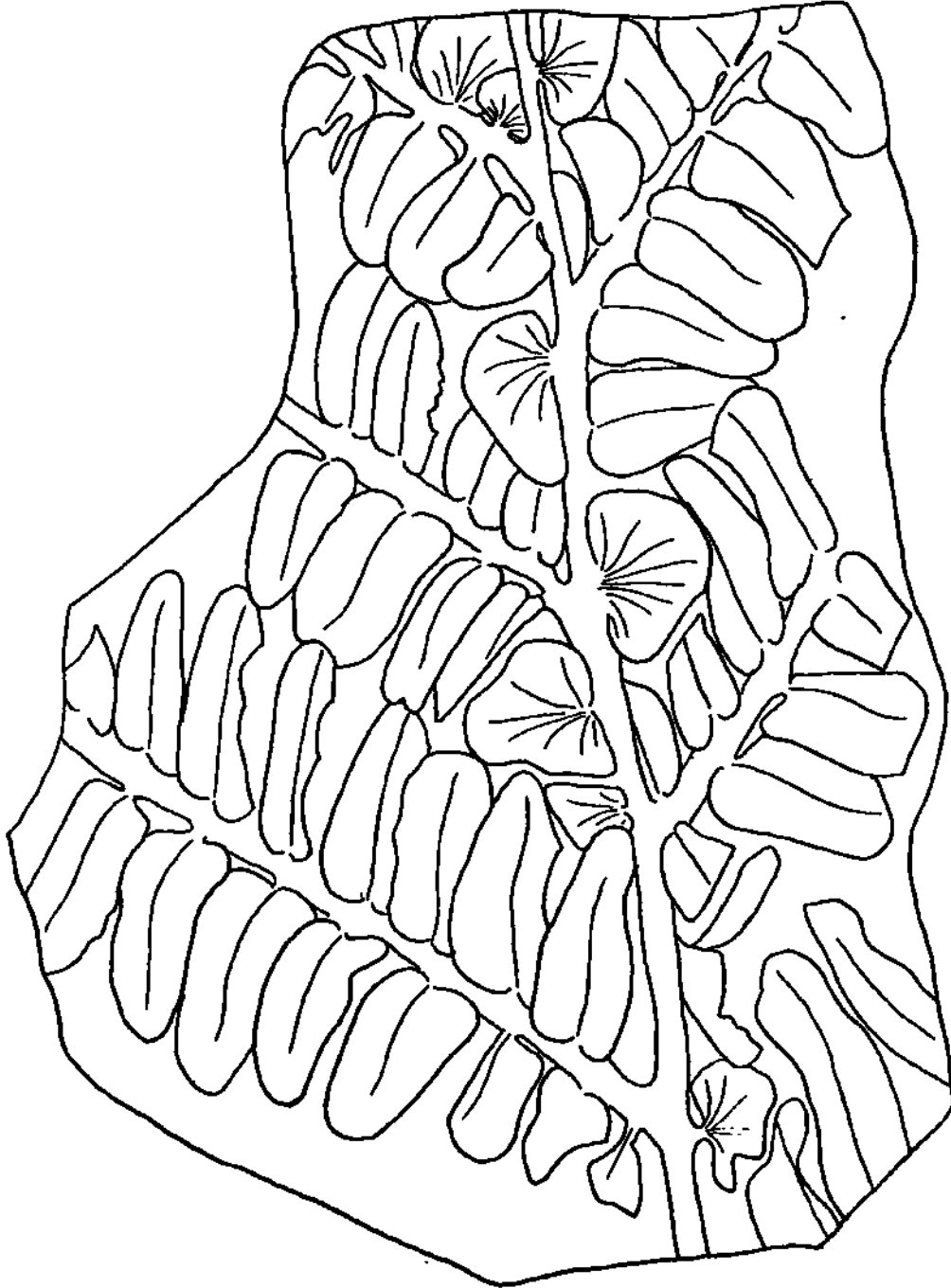
This species occurs in the Transition, Middle, and Lower Coal Measures, but is not common.

## NBURPTBRIS VILLIERSII Brongn.

1828. *Neuroptens' Villiersii* Hrongniart, Ilistoire des Ve\*g6taux fossiles, p. 233, p. 1 64.

Schimper (18, vol. i. p. 444) considers this species to be the apical portion of a frond, of which *JV. auriculata* forms the main portion. Schimper is

FIG. 5 a.

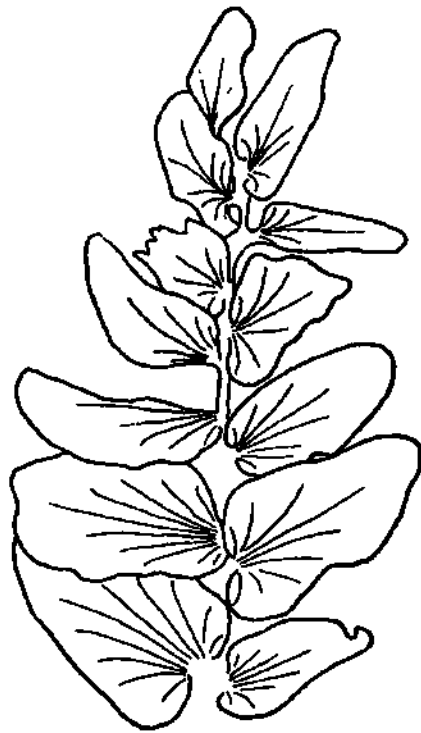


*Neuropteris auriculata* Brongn. (reduced).

quite right in his conclusions, for a careful study of the two species shows no characters by which they can be separated specifically. The geologic<sup>31</sup> distribution is the same for both.

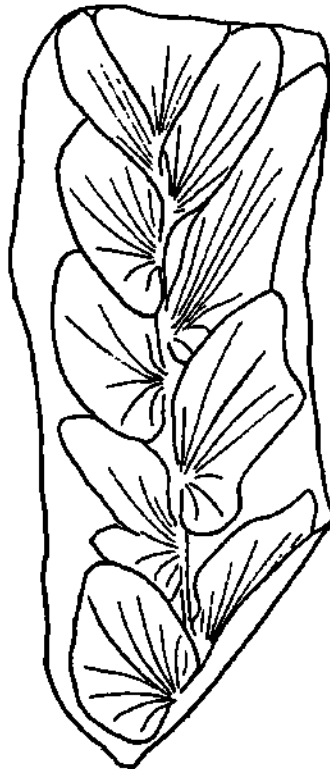
**NEUROPTERIS** OSMUNDS Artis (sp.).  
 1855. *Fdicites Osmund\** Artis, *Antediluvian Phytology*, p. 17.  
 This species does not show any real differences by which it can be separated from *IV. Villiersii* Brongn. and *N. avrintina* Brongn. It is so similar in character to *N. Villiersii* Brongn. that I do not hesitate to place it with that species as an apical portion of *N. auriculata* Brongn. The size, texture, and venation of the pinnules are the same in both cases.  
 The geological distribution is the same for the three species.

FIG. 5 h.



*Neuropteris Osmundta* Artis (a).  
(reduced).

FIG. 5 c.



*Neuropteris Villiersii* Brongn.  
(reduced).

**Conclusions** drawn from a critical study of the Species-group *N. AURICULATA*.  
*N. auriculata* Brongn. was a large frond, bearing numerous cyclopteroid pinnules on a thick rachis, while the apical portions of the frond were of the type now identified as *IT. Villiersii* Brongn. and *IT. Osmundta* (Artis).  
 The characteristic type of venation, in which most of the veins arise directly from the rachis entering the pinnule through the broad point of attachment, a character shared with the genus *Odontopteris*. Potonic (16) suggested the name of *Neurodontopteris* for those forms of *Neuropteris* pinnule which show affinities with *Odontopteris*.

*Characters of Species-group N. AURICULATA.*

The pinna\* have large overlapping pinnules attached to the nidus by a portion of the base, through which many of the veins enter the pinnule after rising in the rachis. In shape the pinnules are broadly oblong with a rounded apex. The veins are moderately fine and numerous.

*Other species of NEUROPTERIS.*

The following species of *Neuropteris* are remarkable for having either a dentate or crenulate margin, a character which at once distinguishes them from any other species of *Neuropteris*. In no case does this type of leaf-margin appear to be due to a partial decay of the lamina. The species are *N. crumulata* Brongn. and *N. dentata* Lesq., and, although occurring in the British Coal-Measures, they are rare and, when found, are usually in a fragmentary condition. Zeiller (21, p. 233, pi. 2G. fig. 1; pi. 27. figs. 5, 6) gives figures of specimens in which some of the pinnules have entire margins. Until more material has been obtained, I do not think it will be possible to ascertain with any degree of certainty the exact relationship existing between these dentate forms and the better-known forms with entire margins.

## CYCLOPTERIS.

Many of the *Neuropteris* fronds had appendages to the rachis which were of a leafy character. These appendages are known as "Cyclopteris." The form of pinnule known as *JS\ fimbriata* Lesq. was also probably an appendage on the rachis. As Seward (19, vol. ii. p. 526) suggests, they may be of the same nature as *Aphlebium*. These *Cyclopteris* pinnules have been long known, but as they are usually found detached from the petiole, it is difficult to say to which species of *Neuropteris* the various kinds belong. They vary in size from very small forms 1 cm. or less in diameter up to 10 cm. or more. The venation of these *Cyclopteris* pinnules differs considerably from that of normal *Neuropteris* in that all the veins radiate from the point of origin of the lamina. This type of venation is seen to a certain extent in some of the pinnules found amongst the species included in the species-group *N. obtusipinna*. The possession of *Cyclopteris* pinnules, however, is not confined to members of that species-group, and they are found on other species, as, for instance, on the petioles of *N. gigantea* Sternb. in the species-group *JV. flexuosa*.

## 5. SUMMARY AND CONCLUSIONS.

As a result of this research it is now possible to state with great precision the relationships existing between the species of *Neuropteris* commonly found in the British coalfields. The species can be divided naturally into three large groups, each of which has one definite type-species.

round which the remainder can be grouped. The groups which I call  
 are identified by the type-species; thus the first group is  
 species-group *N. flexuosa*. Although each species-group is distinct  
 others, yet they are all connected with each other by species  
 characters common to two of the groups. These connecting-links  
 intermediates, which also occur connecting the species within a species-  
 group have always been a source of trouble to workers on the genus, on  
 account of the difficulty of identification. I suggest, therefore, that the  
 most satisfactory method of identifying these intermediates,  
 is to clearly indicate the two "species" between which they are intermediates  
 as an intermediate between *If. flexuosa* and its varietal form  
 identified as *N. flexuosajgigantea*.  
 Each species-group has its own definite and constant characters by which  
 they can be identified, and the members themselves  
 of the characters, which are subordinate to the characters  
 of a species as a whole.  
 I have seen only of a large number of specimens of *Neuropteris*,  
 a greater number of so-called  
 species in the true sense of the word, but are varietal forms  
 and are dependent for their characters on their  
 position on the rachis and, perhaps, to a certain extent on their  
 environment. The species of *Ifeuropteris* under discussion appear to be  
 varietal forms of species:—*N. flexuosa* Sternb., *N. obliqua* Brongn.,  
*N. auriculifera* Brongn., each of which is the type of a species-group.  
 The species of *Neuropteris* should, therefore, be identified as forms of  
*N. gigantea* Sternb. become *N. flexuosa* Sternb. forma  
 This method would give a much clearer idea of the relationships  
 between the various forms of *Neuropteris* pinnule.  
 It is seen that only a few factors in mind the facts that  
 factors which determine the development and structure of  
 each part of the frond, but we can hope to correlate the fragments of pinnule  
 into an unit of the whole frond, and thus obtain a clear  
 knowledge of specific identity. I have endeavoured with these facts  
 constantly in mind to sort out and bring into their true relationship most of  
 the common species of *Neuropteris*. Bunbury (7, p. 248) was undoubtedly  
 correct when he said that we are exceedingly liable to create false species  
 from material which originally grew from the same root.

*Geological Distribution of Species.*

	Upper.	Transition.	Middle.	Lower.
<i>Seuropteris flexvom</i> . . . . .	X	X	X	X
<i>JV. ovata</i> . . . . .	X	X	X	X
<i>N. gif/antea</i> . . . . .	X	X	X	X
<i>N. tennifolia</i> . . . . .	X	X	X	..
<i>N. macrophyU.il....</i> . . . . .	X	X	X	..
<i>N. SchencJizpri</i> . . . . .	X	X	..	..
<i>N. hetcrophylla</i> . . . . .	X	X	X	X
<i>N. rarinerris</i> . . . . .	X	X	X	..
<i>N. obliqnn</i> . . . . .	X	X	X	X
<i>JV. callosa</i> . . . . .	..	X	X	..
<i>N. Schlehani</i> . . . . .	..	X	X	X
<i>N. rectinervis</i> . . . . .	..	..	X	X
<i>N. auriculata</i> . . . . .	..	X	X	X
<i>N. Villiersii</i> . . . . .	..	X	X	X
<i>N. (hmunda</i> . . . . .	..	X	X	X

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"
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NEUROPTERIS TKNUtKOLLA.



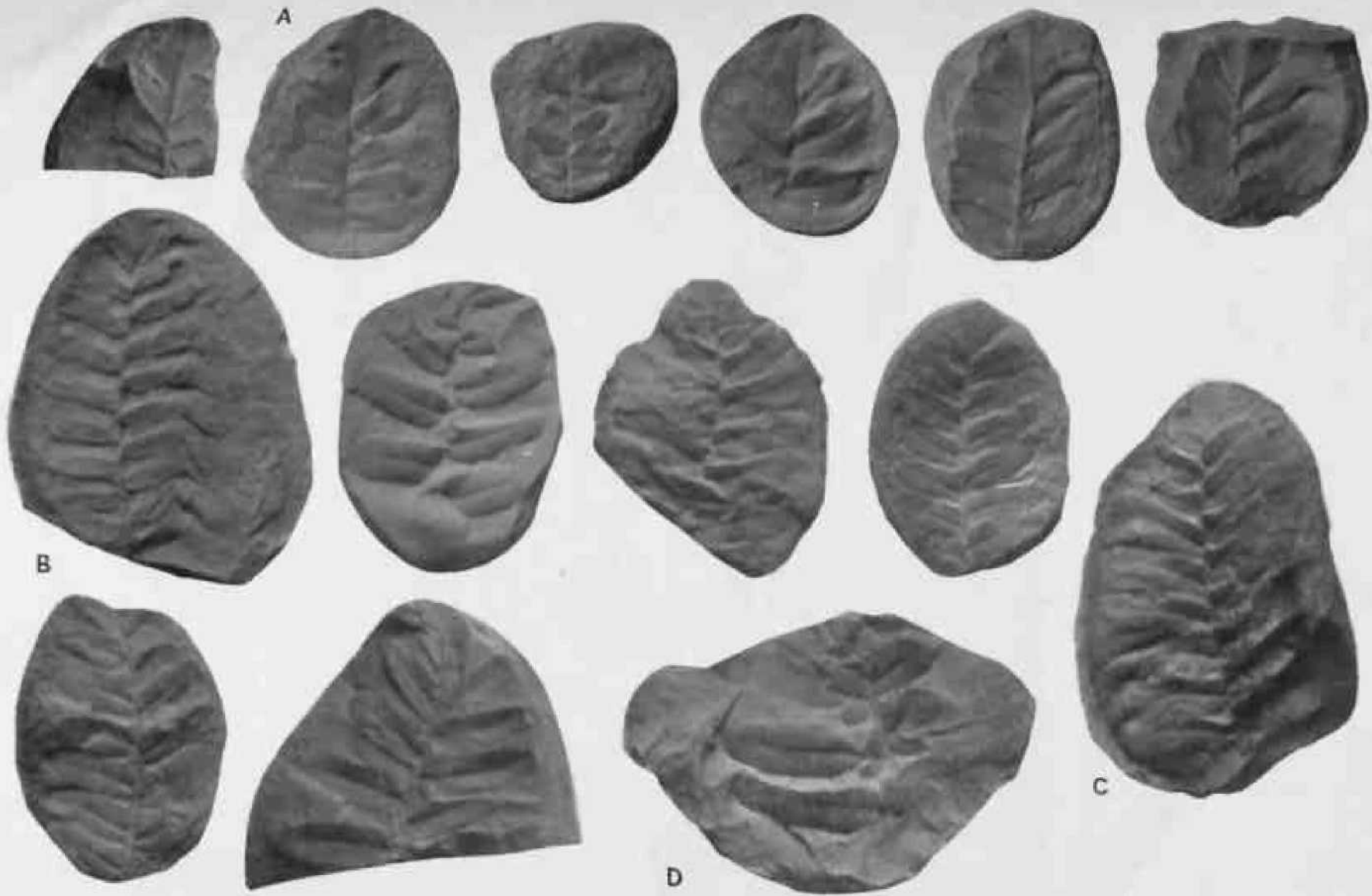


Photo. by J. W. TUTCHER.

SPECIES AND TMTERMEDIATES OF KEUHOPTEH1S FLKXUOSA.

CERTAIN SPECIES OF THE GENUS NBUBOPTEBIS.

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- a———' Flore Fossile de terrain houiller de Commentry. 1 «\* .

EXPLANATION OF THE PLATES.

PLATK 6.

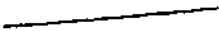
A specimen of *Neuropterii tenuifolia* Schloth., -with some of the pinnate lateral pinn», showing the characters usually associate with *N. tenuifolia* Sternb. X 009.

PLATE 6.

A series of specimens from Crawcrook, showing • P " J<sup>1</sup> « Id intermedlftte8 belonging to the Species-group *N. Jkxuom.* X . 66.

A. - ^ . fe. *Tuosa* Sternb.; B. - K W «» ^ « Stemb., C ~ A > *tenuifolia* Schloth.; D.—*N. macrophylla* Bionga. row being

The rest of the specimens are intermediates; those ii' \*e ^ ^ etween intermediate\* between A and B; those in the second row B and C, and those in the bottom row between C ana u.

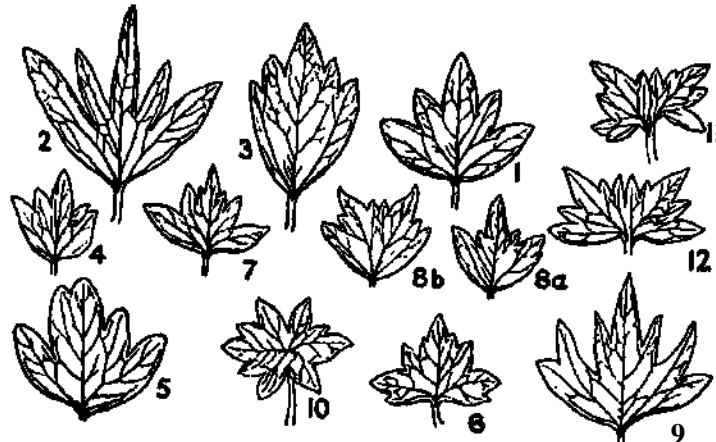




their development on the central lobe only is shown. They may be little more than slight outgrowths of the lobe-margin as in the asymmetrical case shown in fig. 8a, or be strongly developed as shown in fig. 10. There is no indication of co-ordination between the two cotyledons of the same seedling > the development of these accessory lobes, though where they are developed in one they are at least represented in the other. A small accessory lobe on one lateral lobe is shown in Lubbock's figure (9, fig. 223), whilst they are well developed on all the lateral lobes of the seedling figured by Marshall Ward (W, fig-159). Kerner's figure shows a slight one on one of the median lobes only (8, fig U<sub>8</sub>).

As frequently happens when a large series of seedlings is collected, a few specimens, exhibiting some degree of abnormality were obtained; these included both syncotyls and polycotyls. Of the latter, one (fig-10) was

Figs. 1-12.



Variations in the morphology of the cotyledon

amphisyncotylous and showed suppression of an intermediate lobe in one cotyledon whilst the other (fig. 12) showed a lateral spot which had resulted in the reduction of the lobes on the symphysis side. The polycotyls were two in number, namely a hemitricotyl and a tricotyl, the cotyledonary members of the former being shown in figs. 8 a, 8 b.

HISTOLOGY.

The cotyledon hairs clothed the seedling of two kinds and show well-marked differences in distribution. Most of them are unicellular and end in an acute point (fig. 13), occasionally a single transverse wall may be present. The hairs of this type are scattered, but in the cotyledons they are confined to the areas between the veins and to the petioles as an epidermal outgrowth, but those on the upper surface differ from those on the lower surface in being slightly raised (fig. 14). The latter are composed of cells which form a base of the hair in many cases appears to

practically square when seen in plan, but in other cases it is elongated in the direction of the path of the vein over which it lies (fig. 15). The walls are slightly lignified and give a pink reaction with phloroglucinol after oxidation with hydrochloric acid.

The second type of hair, which is multicellular and club-shaped (fig. 16 a), is much less abundant and only occurs on the upper surfaces of the cotyledons between the veins and on the inner faces of the cotyledonary petioles. Each consists of a relatively stout stalk composed of two or three superposed cells above which is a central region showing four cells in transverse section (fig. 16 b). Succeeding this is a two-celled region (fig. 16 c), which in turn is capped by a single cell. This may be either practically hemispherical or broadly wedge-shaped with a convex free surface.

Figs. 13-16.

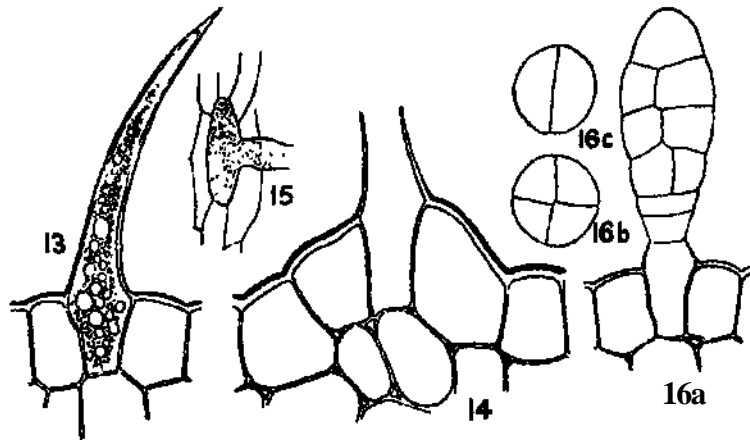


Fig. 13. A pointed unicellular hair from the lower epidermis of the cotyledon; the majority are considerably longer than the one figured. Fig. 14. Base of a hair from the upper epidermis of the cotyledon, to show the larger epidermal cells and the slightly raised base of the hair. Fig. 15. Elongated base of a hair in surface view. Fig. 16 a. Club-shaped hair in longitudinal and transverse sections. The cell contents of the hairs, which are similar in all, are only shown in fig. 13.

The cells of both types of hair are crowded with bright yellow globules of oil (fig. 13). These have the appearance of oil-droplets, but do not give reactions characteristic of fatty substances. They are insoluble in alcohol, chloroform, ether, and xylol and are unaffected by ether acids or alkalis. We have been unable to determine their precise nature, but their resistance to the action of solvents is a point of some interest.

The cells of the upper epidermis are polygonal in surface view and are distinctly larger than those of the lower epidermis (c/. figs. 13 & 14). The walls of the upper epidermis are thicker than those of the lower epidermis, which resemble the lower epidermis in character (fig. 14). The stomata are similarly situated on the upper surface. The stomata are of a similar character to those on the lower surface and are remarkable for their variation in size. The

types are recognisable, the first of which is relatively large and is ovoid in plan, whilst the second is much smaller and is almost circular in plan (fig. 17<sup>a</sup>). Among the smaller type a few examples of twinned stomata have been observed, one of which is shown in fig. 17<sup>b</sup>.

Scattered through the cortex of the cotyledonary petioles and of the hypocotyl and roots are cells containing mucilage, these standing out clearly after staining.

FIG. 17.

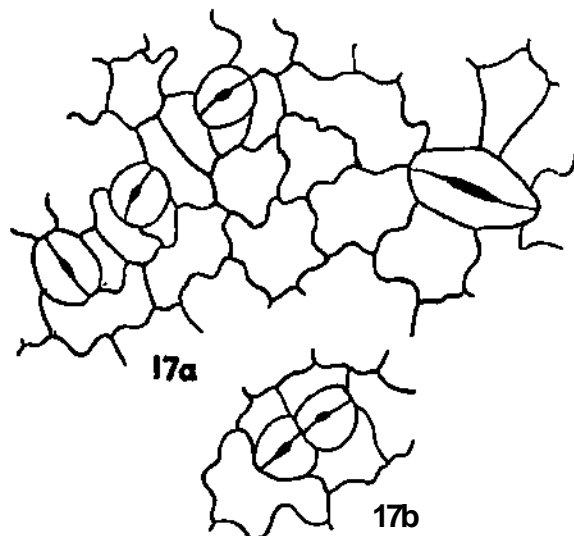


Fig. 17 *a*. Portion of the lower epidermis from the cotyledon, to show the variation in the size of the stomata. Fig. 17 *b*. The same showing twinned stomata.

The yellow fat-like globules occurring in the epidermal hairs, to which reference has already been made, are abundant in the bundle-sheath and the adjacent layers of the hypocotyl, petiole, and root, and are also present in the medullary parenchyma. They are rare or absent in the cortical cells.

#### THE VASCULAR SYSTEM.

The midrib of the cotyledon is a collateral bundle which becomes somewhat extended tangentially following its junction with the bundles from the intermediate lobes. This increase in width becomes more pronounced as a result of the incoming of the strands supplying the lateral lobes. The union of the laterals with the midrib may occur at or near the base of the lamina or at various levels in the petiole. In the composite bundle thus produced, although the phloem forms a continuous mass, it is possible in young seedling<sup>9</sup> to differentiate the midrib xylem from that of the lateral lobes (figs. 18, 19, 20), although this becomes impossible in older seedlings. The characteristic triad structure, with its central file of xylem elements flanked by separate phloem groups, is not shown in the petioles of even the youngest seedlings examined, the phloem being continuous. A very frequent feature in the upper part of the hypocotyl is one in which the metaxylem, as seen in

transverse section, forms two fan-shaped masses, one on either side of the Protoxylem. Occasionally the metaxylem elements nearest the protoxylem curve over this and, in the younger seedlings, as a result, isolated metaxylem vessels may be seen above the protoxylem in the cotyledonary plane (fig. 20).

FIGS. 18-20.

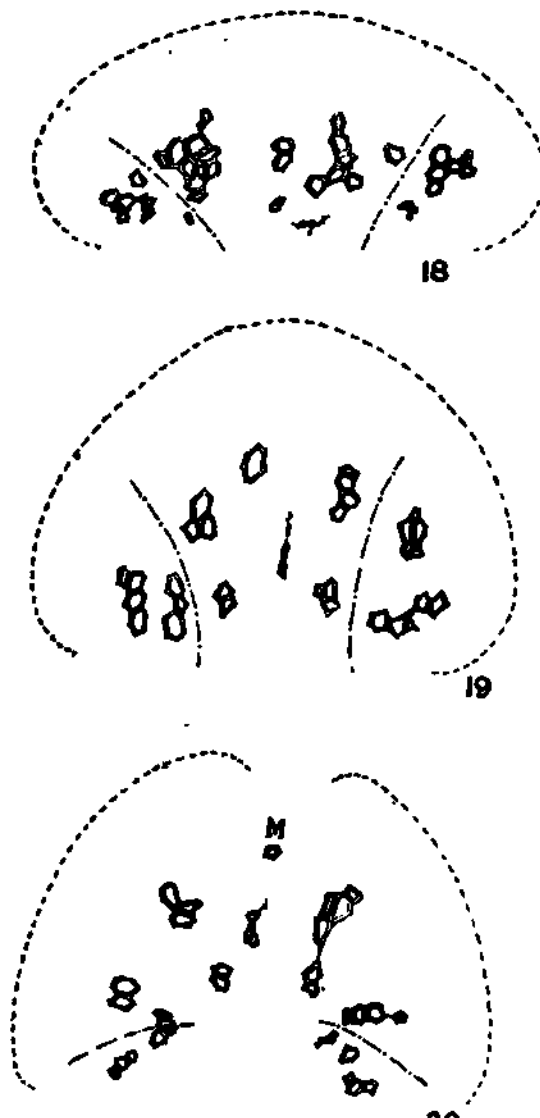


Fig. 18. Transverse section of the cotyledonary midrib after union with the lateral strands.  
 \*%• 19. The same at the top of the hypocotyl. Fig. 20. The same in the middle of the hypocotyl. Note the isolated metaxylem element (M) above the disorganising protoxylem in the cotyledonary plane. Xylem only shown, phloem indicated by plain dotted line, junction of lateral strands and midrib indicated thus———

The epicotyledonary strands play no significant part in transition. As is the case in the Sycamore (*Acer Pseudoplatanus*) (13) the behaviour varies, the types noted being as follows :—

- \*• The phloem bifurcates and unites with that from the cotyledons, whilst the xylem dies out *in situ*.

2. Both phloem and xylem divide and unite with the corresponding elements from the cotyledons.

3. The strand moves as a whole to unite with the cotyledonary strand.

The transition to typical tetrarch root-structure is extremely leisurely. The lateral xylems separate from those of the midrib (fig. 20) more and more widely and finally unite in the lower half of the hypocotyl. Here develop groups of protoxylem and form typical secants in the cotyledonary plane. Actual root-structure is only attained some distance below the collet. A small medulla is present throughout the root.

Although the sequence described above holds good for the majority of seedlings examined a number of interesting variations have been encountered. The simplest of these, and one which does not in any way affect the root structure, is produced by the complete independence of the lateral veins which at no part of their course come into contact with the midrib bundle. This type of transition, which occurs only in one seedling, is typical of many other species such, for example, as *Impatiens Roylei* (10,11).

A second variant, also represented by one seedling only, has resulted in a condition directly opposite to that described above. In this case the lateral strands of one side in each cotyledon become completely merged with the midribs and do not again separate. The result is that in the root, two of the poles being derived from the midribs and one from the two laterals which behave normally. The transition phenomena in this seedling are reminiscent of those described by Oompton (3) for *Porycnium hirsutum* allowance being made for the fact that the latter is a species with independent lateral strands.

Still a third variant, in this case represented by two seedlings, is one in which the root is pentarch. In one of these seedlings the earlier part of the transition is quite normal. Following the complete separation of the laterals, however, the two on one side, instead of uniting, continue down the hypocotyl as independent collateral strands. These gradually flatten out and form tangentially extended plates and, just above the collet, develop separate protoxylems in an exarch position. The phloems bifurcate just prior to the appearance of the new protoxylems, and form typical groups by lateral union with adjacent groups. The second example is one in which the whole of the transition to root-structure is perfectly normal, so that the root is prima tetrarch. In the lower portion of the root, however, a small group of metaxylem vessels becomes separated off from one of the intercotyledonary poles and moves laterally. The phloem group which overarches it then divides and an exarch protoxylem is developed opposite the gap thus formed, so producing a pentarch condition. It seems reasonable to regard this second example as one in which the independence of the laterals as pole-forming units is asserted relatively late in the transition, so that its difference from the first example is one of degree rather than kind.



With regard to the abnormal seedlings, only one of the syncotyly showed vascular abnormality, this being the one in which the unilateral syncotyly was most marked. As a result of compression the vascular strands supplying the lateral lobes on the symphysis side unite with the midribs precociously. This union is permanent so that only the two midribs and the second pair of midribs form the root as a consequence being triarch.

The hemitricotyly (fig. 8 a, b) and tricotyly were both pentarch, but in these the pentarchy has a totally different origin from that occurring in the dicotyly ascribed in an earlier portion of this paper. In both cases the midrib strands each formed a root-pole, the two remaining poles being produced by the lateral strands. These in one cotyledon behaved quite normally, gratifying from the compound central strand and uniting with similar strands from the adjacent cotyledons, thus producing two further poles. In the hemitricotyly the suppression is due to the complete merging of one of the midribs in each of two cotyledons with the midrib. In the tricotyly the adjacent lateral lobes along the line of junction of the two imperfectly stratified strands are not developed and, as a consequence, the lateral midribs which would normally supply them are non-existent.

DISCUSSION.

Although a considerable body of work on seedling anatomy has now accumulated it has not yielded the clearly defined information regarding phylogeny which it was hoped would accrue. All the same a number of interesting results have been obtained, and it is reasonable to assume that the continued pursuit of seedling investigation a satisfactory conception of the features which characterized the ancestral types will be possible.

Miles Thomas has already summarized certain aspects of her extended work in a recently published report (15), and her fuller account will be looked for with considerable eagerness. One fact which does emerge clearly is that the variations in seedling anatomy are due not to a great number of fundamentally different basic types, but rather to a series of changes on the components of a common group of vascular constituents of this common group, the chief of which are the midrib and serais, may undergo, in different seedlings, changes with regard to linkage, fusion or independence, and in importance or position. Where, as sometimes happens, a new factor of variation Picotyledonary strands plays an important part a further series of changes is rendered possible (7).

The commonest type of vascular arrangement is tetrarch in which the midrib and its lateral strands remain independent of the site conditions which they constitute a compact median compound structure. It has been recorded and briefly described by

Thomas (U) for *Althaea*, and De Fraine for *Opuntia mxdXopaUa* (6).

*Tilia* furnishes an example of an intermediate condition since, although the fusion of the phloem system of the median and lateral strands is complete, the union of the xylem strands is relatively loose and is rather in the nature of a close linkage than a merging of identity. The fact that *Tilia* exhibits a type of transition in which the laterals remain independent throughout is worthy of note in this connection. Such a condition is relatively rare in *Tilia*, but other species such as *Pyrus communis* (14) show a large degree of variability. *Tilia* shows some approach to *Pyrus communis* also in the fact that the laterals may assume a more important role in root-pole formation, each forming a pole independently instead of uniting to form a common pole. In *Tilia* the condition is unilateral so that pentarchy results, whilst in *Pyrus* both sets of laterals may be involved, thus leading to a hexarch root condition.

Miss Bexon, who has recently made an intensive study of *Althaea* (1) has shown that in this case also a considerable amount of variation occurs producing a tetrarch-hexarch range in the root, so that in the case of that genus a more extended comparison with *Pyrus* is possible.

The reverse condition, in which a reduction from tetrarchy to triarchy occurs, is frequent in the Leguminosae, and Oompton (3) interprets this with some degree of probability as illustrating a tendency towards reduction to diarchy from an ancestral tetrarch condition.

It is remarkable that, in *Tilia*, such a reduction may occur in what appears to be an absolutely normal seedling, and this renders one less confident in ascribing to compression the loss of a pole in the syncotyl described earlier. At the same time there is a considerable body of evidence (4,10,11) that in compression consequent on unilateral syncotily does lead to a lessening of the importance of the lateral strands on the symphysis side, and it may be that in *Tilia* a rarely expressed potential reduction is rendered more frequent by such a compression.

We are perhaps on safer ground in ascribing the suppression of one of the intercotyledonary poles of the tricotyl to crowding, as it is characteristic of the majority of polycotyls to find the number of poles reduced from what one would expect by comparison with the normal seedling.

In an earlier paper on polycotily (12) it was suggested that the division of the meristem which resulted in the hemitricotylous and other polycotylous states might be either qualitative or quantitative. If the former, the midribs of the two resultant cotyledons would behave in transition like a single normal midrib; if the latter, then each of the daughter midribs would show triad structure and exhibit a certain degree of independence in transition. If this conception is sound, the hemitricotyl and tricotyl of *Tilia* described above both have resulted from an apical division of the quantitative type-

SUMMARY.

1. The seedlings of *Tilia vulgaris* possess two typically five-lobed epigeal cotyledons.
2. The cotyledons vary in size and may show elongation or shortening compared with a common mean type. They may also develop accessory lobes.
3. The aerial parts are thinly pubescent, the hairs present being of two types: (a) Cellular ones confined to the epidermal ridges above and below the vascular laminae but generally distributed over the surface of the cotyledons between the veins.
4. The vascular system is atrich in plan and typical root-structure is only a short distance below the collet.
5. Seedlings showing triarchy or pentarchy also occur. In some dicotyledonous seedlings, where the syncotily is unilateral and at all points pronounced, showing triarchy or pentarchy.
7. The polycotylous seedlings examined are pentarch, though the pentarchy in this case is not homologous with that occurring in dicotyls.

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The Vascular Supply of the Bracts of some Species of *Anemone*\*. By  
 A. EVELYN OHESTERS, M.S.C, University College, Nottingham. (Com-  
 municated by H. S. HOLDEN, D.Sc, F.L.S.)

(PLATES 21-36, and 9 Text-figures.)

[Read 18th November, 1926.]

INTRODUCTION.

THE Ranunculaceae, being held by the majority of modern systematists to form a relatively primitive order, have been regarded as a group from which some suggestion as to the origin of perianth in flowers might be obtained. In this connection four types of "leaf" come under consideration: (a) the so-called "honey leaves"—"leaf-structures of the flower, the essential function of which lies in honey secretion" (6); (b) corolla; (c) calyx; (d) bracts. The derivation of honey leaves from stamens by a process of sterilisation appears to be a generally accepted fact, but there is a difference of opinion as to what structures should be included under the term "honey leaves". Many botanists restrict this term to the small staminodal structures of certain species of *Clematis* and the more typical honey leaves such as are present in *Eranthis*, while Prantl (6) also includes the large petaloid leaves of *Aquilegia* and species of *Ranunculus* which are usually termed corolla.

Concerning the origin of calyx and corolla, there are two principal hypotheses to be noted. Worsdell (11), on the one hand, considers that "honey leaves" are a transitional stage in the modification of stamens to form petals—these, again, by further modification, giving rise to sepals. Worsdell, indeed, derives not only corolla and calyx but also bracts and foliage leaves from a sporophyll by this process of sterilisation, thus pushing the "sterilisation theory" of sporophytic elaboration outlined by Bower (2) to its extreme limit.

Prantl (6), on the other hand, draws a sharp distinction between honey leaves and true perianth leaves, and regards the perianth in the Ranunculaceae as being of foliar nature, preferring the terms "bracteoid" and "petaloid" perianth leaves to "calyx" and "corolla." This derivation of perianth leaves from bracts is upheld by Salisbury (9) as the result of a statistical study of members of the Ranunculaceae. On this view, therefore, part of the perianth at least is regarded as produced by the modification of foliage leaves, involucre bracts being a transitional stage in this process.

\* Thesis accepted for the degree of M.Sc. in the University of Liverpool.



In this connection the genus *Anemone* is of particular interest, since it possesses a very characteristic involucre of three bracts surrounding the flower stalk, and shows marked variations in both position and form of the involucre in different species. In some, notably *A. Hepatica*, the involucre in form and function closely approaches a typical calyx such as is found in *Ranunculus Ficaria*, whilst in others (*A. nemorosa*, for example) it is distinguishable from the foliage leaves only by its position.

Existing views on the relationship of the involucre of *Anemone* and the calyx of *Ranunculus Ficaria* appear to have been founded on a morphological study of the peduncle and bracts of the numerous species of *Anemone* and of the calyx of *R. Ficaria*, anatomical investigation being almost entirely confined to the rhizome and petiole of *Anemone*. It is possible, however, that an investigation of the vascular supply of the peduncle and bracts of various species of *Anemone*, and of the calyx of *R. Ficaria*, might throw some light on the question of the relationship of these structures, and the present investigation, although of a preliminary nature, has yielded interesting and suggestive results in this connection.

While attention has been specially focussed on the genus *Anemone*, *Ranunculus Ficaria* and *JEranthis hyemalis* have also been studied for purposes of comparison. The species of *Anemone* selected for this investigation—namely, *A. angulosa*, *A. apennina*, *A. blanda*, *A. coronaria*, *A. fulgens*, *A. Hepatica*, *A. japonica*, *A. nemorosa*, *A. Pulsatilla*, *A. pahnata*, *A. ranunculoides*, *A. rivularis*, and *A. sylvestris*—are fairly representative of the various types of bract or "hypophyll" occurring within the genus, and as far as possible normal specimens have been studied.

Oil morphological grounds these species form a series which would appear to illustrate the transformation of the leafy bracts into a typical calyx-like structure, or *vice versa*, a transformation marked by distinct anatomical variation. Before proceeding to the detailed anatomical study, it may be helpful to take a brief morphological survey of the types of involucre occurring in the various species, and to note the kind of foliage leaf which accompanies the different types of hypophyll.

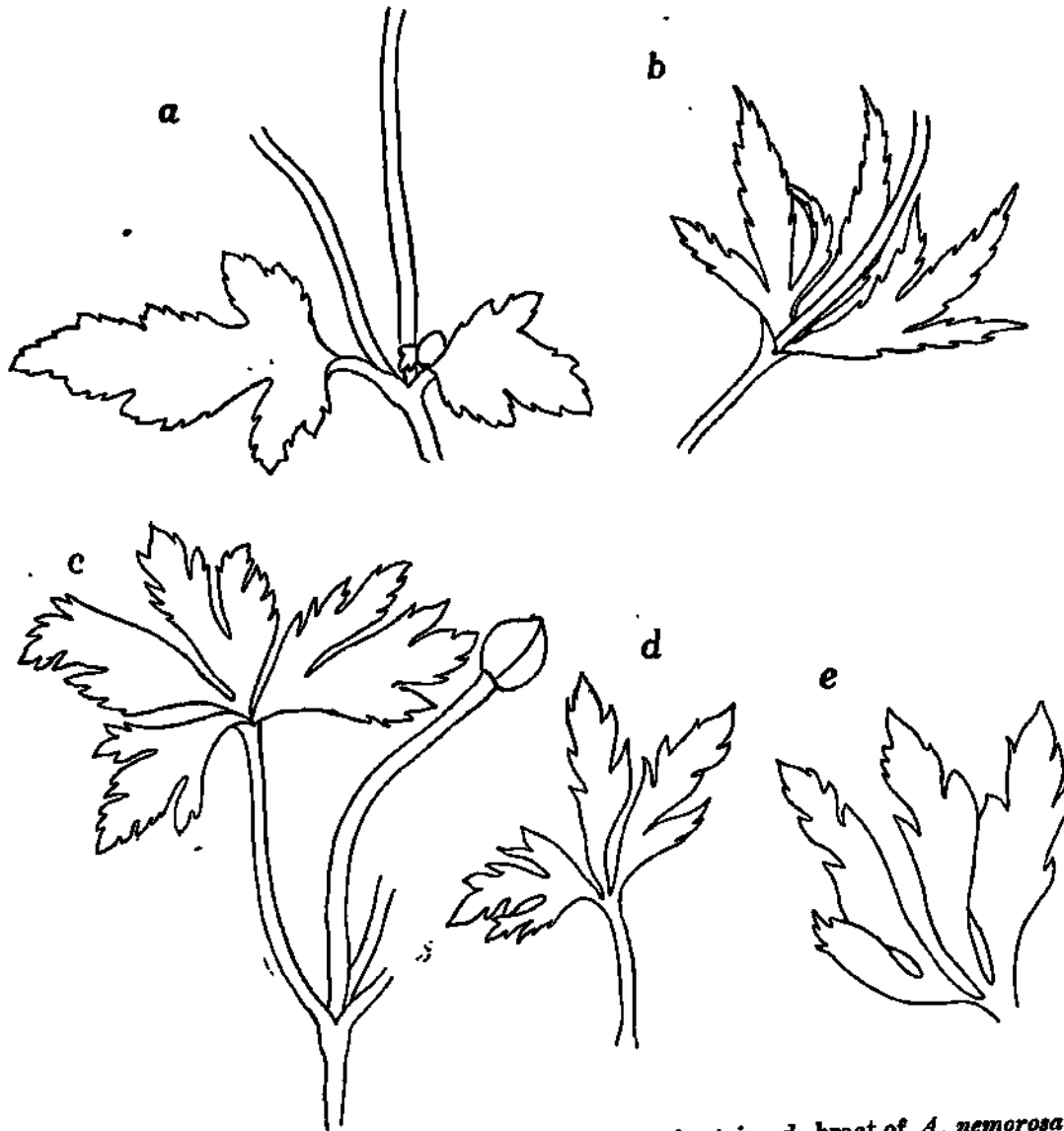
#### POSITION AND FORM OF BRACTS.

*A. japonica* may be regarded as representing one end of the series. The flower axis is erect and branches freely, resulting in the cymose inflorescence which is characteristic of the Order. There is no well-marked involucre of three bracts, but at each node usually two hypophylls arise, each bearing a shoot in its axil. The vegetative leaf consists of a well-developed petiole bearing three short-stalked leaflets. Each leaflet exhibits three main lobes, while the margin is sharply indented. The hypophylls differ from the foliage leaves in the absence of petiole, and, as they are carried well up into the light by the axis, are capable of functioning as photosynthetic organs (text-fig. 1, a).

*A. nivalis* is of the same cymose type, but smaller, and the branching is much more restricted. Both vegetative leaves and hypsophylls are deeply indented. As in *A. japonica*, the hypsophylls—of which, however, there are usually three at each node—are distinguished from vegetative leaves by the absence of petiole (text-fig. 1, *b*).

*A. sylvestris*. The vegetative leaves and hypsophylls consist of a well-developed petiole bearing three sessile leaflets which are slightly segmented.

TEXT-FIG. 1.



*a*, bract of *A. japonica*; *b*, of *A. sylvestris*; *c*, of *A. ranunculoides*; *d*, bract of *A. nemorosa*; *e*, of *A. nemorosa*.

The peduncle bears an involucre of three (rarely four) hypsophylls very similar to the foliage leaves. Axillary buds in axis bearing involucre and flower. The presence of the three-leafed instant feature of the remaining species (text-fig. 1, *e*).

*A. nemorosa*, *A. apennina*, *A. blanda*. These species have <sup>ch in</sup> <sup>nd a</sup> <sup>re</sup> <sup>re of</sup> <sup>ble</sup> <sup>luc</sup> <sup>ho</sup> <sup>very</sup> <sup>t this</sup> <sup>la</sup> common. In each the vegetative leaf consists of three stalked leaflets, a well-developed petiole. Each leaflet is divided into three lobes which are deeply segmented. The flower axis is unbranched and bears an involucre of three hypsophylls. These are large and leafy, and are only distinguishable from the vegetative leaves by position. The internode between <sup>invo</sup> <sup>luc</sup> and flower becomes elongated and the involucreal leaves function as <sup>pho</sup> <sup>to</sup> <sup>synthetic</sup> organs. Although in each species the flower is solitary, <sup>e</sup> <sup>very</sup> <sup>t</sup> <sup>this</sup> <sup>la</sup> specimen of *A. apennina* examined a small axillary shoot was present, becoming evident only in the transverse sections of this region of the <sup>pl</sup> (text-fig. 1, d).

*A. ranunculoides*. The inflorescence is typically solitary, but <sup>cimen</sup> <sup>s</sup> <sup>d well-</sup> <sup>etative</sup> <sup>e is</sup> <sup>b</sup> <sup>y</sup> <sup>ot 5</sup> <sup>or the</sup> <sup>mone,</sup> <sup>present,</sup> <sup>case a</sup> <sup>the in-</sup> <sup>flower</sup> in which two flowers arise from the involucre are not uncommon, and well-developed axillary shoots are of frequent occurrence. Both vegetative leaves and hypsophylls are of the same type as *A. nemorosa*, but <sup>ner</sup> <sup>b</sup> <sup>y</sup> <sup>ot 5</sup> <sup>or the</sup> <sup>mone,</sup> <sup>present,</sup> <sup>case a</sup> <sup>the in-</sup> <sup>flower</sup> decided reduction in the length of the hypsophyll petioles, accompanied by broadening of the leaf-base (text-fig. 1, e). In one of the specimens <sup>exal</sup> <sup>ot 5</sup> the axis exhibited the usual three-leaved involucre, but the axillary <sup>s</sup> <sup>or the</sup> <sup>mone,</sup> <sup>present,</sup> <sup>case a</sup> <sup>the in-</sup> <sup>flower</sup> were particularly well developed, one producing two leaves and a <sup>now</sup> <sup>or the</sup> <sup>mone,</sup> <sup>present,</sup> <sup>case a</sup> <sup>the in-</sup> <sup>flower</sup> other two small leaves. It is interesting to note that in species of *Ane* <sup>mone,</sup> <sup>present,</sup> <sup>case a</sup> <sup>the in-</sup> <sup>flower</sup> where the inflorescence is typically solitary, if axillary shoots are <sup>p</sup> <sup>resent,</sup> <sup>case a</sup> <sup>the in-</sup> <sup>flower</sup> two (and not three) leaves are usually produced, even when, <sup>a3</sup> <sup>in this</sup> <sup>case a</sup> <sup>the in-</sup> <sup>flower</sup> flower also arises. It may be noted that in *A. sylvestris*, where <sup>t</sup> <sup>he in-</sup> <sup>flower</sup> the inflorescence is cymose more frequently than solitary, the axillary <sup>flower</sup> bearing shoots exhibit the usual three-leaved involucre.

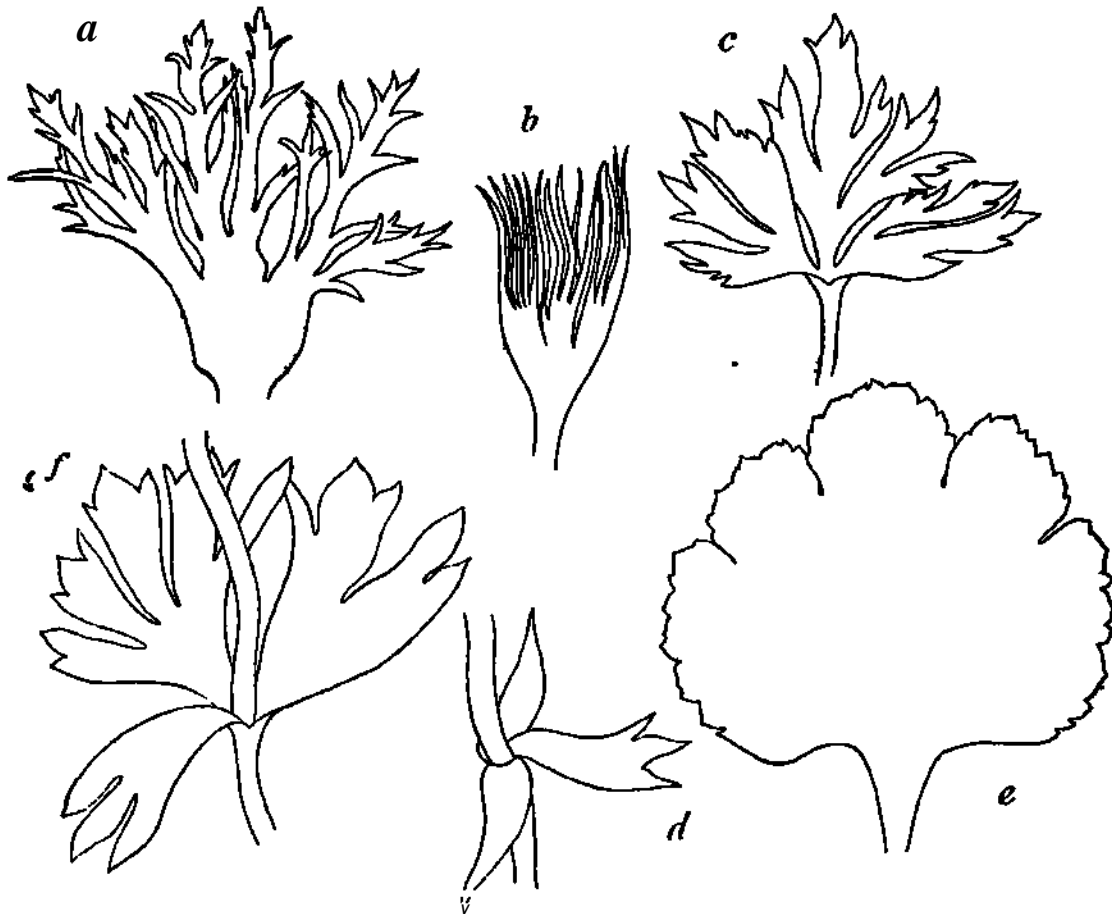
-4. *coronaria*. The foliage leaf has a petiole several inches long <sup>d th</sup> <sup>e</sup> <sup>m an</sup> <sup>illary</sup> <sup>h in the</sup> <sup>The</sup> <sup>is</sup> <sup>early</sup> <sup>the</sup> <sup>lateral</sup> <sup>quite</sup> <sup>in the</sup> <sup>a</sup> <sup>is</sup> and the lamina consists of three much divided leaflets. The flower arises from <sup>m an</sup> <sup>illary</sup> <sup>h in the</sup> <sup>The</sup> <sup>is</sup> <sup>early</sup> <sup>the</sup> <sup>lateral</sup> <sup>quite</sup> <sup>in the</sup> <sup>a</sup> <sup>is</sup> an involucre of three bracts, and, though the inflorescence is solitary, two <sup>a</sup> <sup>illary</sup> <sup>h in the</sup> <sup>The</sup> <sup>is</sup> <sup>early</sup> <sup>the</sup> <sup>lateral</sup> <sup>quite</sup> <sup>in the</sup> <sup>a</sup> <sup>is</sup> axillary shoots may occur. Frequently one or two additional bracts arise with <sup>h in the</sup> <sup>The</sup> <sup>is</sup> <sup>early</sup> <sup>the</sup> <sup>lateral</sup> <sup>quite</sup> <sup>in the</sup> <sup>a</sup> <sup>is</sup> the typical involucre. The bracts are sessile, with a very broad leaf-base, <sup>The</sup> <sup>is</sup> <sup>early</sup> <sup>the</sup> <sup>lateral</sup> <sup>quite</sup> <sup>in the</sup> <sup>a</sup> <sup>is</sup> lamina is segmented, but to a less extent than the foliage leaves. In <sup>is</sup> <sup>early</sup> <sup>the</sup> <sup>lateral</sup> <sup>quite</sup> <sup>in the</sup> <sup>a</sup> <sup>is</sup> its early stages the sheathing bracts closely surround the flower-bud. Later <sup>the</sup> <sup>lateral</sup> <sup>quite</sup> <sup>in the</sup> <sup>a</sup> <sup>is</sup> the internode elongates about an inch or an inch and a half, and the <sup>invo</sup> <sup>lateral</sup> <sup>quite</sup> <sup>in the</sup> <sup>a</sup> <sup>is</sup> involucreal leaves take up a horizontal position. The hypsophyll here is <sup>thus</sup> <sup>quite</sup> <sup>in the</sup> <sup>a</sup> <sup>is</sup> quite distinct in appearance from the vegetative leaf, the difference <sup>lyi</sup> <sup>g</sup> <sup>in the</sup> <sup>a</sup> <sup>is</sup> being a greater development of the leaf-base and a reduction of petiole and lamina <sup>a</sup> <sup>is</sup> i. e., the adequacy of the hypsophyll as a protective sheathing organ <sup>is</sup> developing at the expense of its photosynthetic capacity (text-fig. 2, a).

*A. Pulsatilla*. The vegetative leaves are of the usual divided type. <sup>The</sup> <sup>lateral</sup> <sup>quite</sup> <sup>in the</sup> <sup>a</sup> <sup>is</sup> The involucre closely envelops the flower-stalk. Each bract consists of a broad <sup>base</sup> <sup>and a lamina</sup> <sup>of three lobes,</sup> <sup>which are divided</sup> <sup>into a number of</sup> <sup>single</sup> <sup>like</sup> <sup>segments.</sup> <sup>The bases</sup> <sup>of the bracts</sup> <sup>unite</sup> <sup>and form</sup> <sup>for a short distance</sup> <sup>a coherent sheath</sup> <sup>round the axis,</sup> <sup>The flower</sup> <sup>is solitary</sup> <sup>and no</sup> <sup>axillary</sup>

shoots have been observed. The bracts form a more effective sheath for a longer period than in any of the species commented on above, and even when fully developed the internode between involucre and flower elongates to a less extent than in *A. coronaria* (text-fig. 2, b).

*A. fulgens* shows a distinct advance in the series. The vegetative leaves resemble those of *A. nemorosa*, but the segmentation is not so pronounced and the petioles of the leaflets are shorter (text-fig. 2, c). The involucral leaves are sessile, and the internode between involucre and flower becomes elongated. The bracts are of a much simpler type than any so far considered.

TEXT-FIG. 2.



a, flower bud of *A. coronaria*; b, of *A. Pukatiua*; c, foliage leaf of *A. fulgens*; d, involucre of *A. fulgens*; e, foliage leaf of *A. palmata*; f, involucre of *A. ptdmata*.

few, one can be distinguished as the bract  $\wedge \wedge Z'' \pounds \pounds$   $\pounds^R \gg$  bas, bears a small lamina of three entire  $\wedge * ?$  J S L one or both  $\wedge^{ac}$  teoles are typically unsegmented, although occasionally the hypsophylls are typically exhibit slight segmentation. Thus in *A. fulgens* the hypsophylls are of little as photosynthetic organs, their absence or petiole,  $\% \pounds ? * * the$  flower-bud; hence the reduction of lamina, absence of development of base (text-fig. 2, d).

*A. palmata* is an exceptionally interesting type. The vegetative leaf has a simple trilobed lamina with a slightly indented margin (text-fig. 3, a). The involucre leaves are sessile with broad leaf-bases, and exhibit a much more distinct segmentation than do the vegetative leaves. This segmentation, moreover, is not of the same type as that of the vegetative leaves, but that of species such as *A. coronaria*—a fact noted by Salisbury (9)—developed axillary shoots are usually present, consisting of two hypophylls and a flower (text-fig. 2, /).

*A. angulosa* is also characterised by a simple vegetative leaf of three lobes with a slightly indented margin (text-fig. 3, a). The solitary flower arises from an involucre of three bracts, but as the internode remains very short, the

TEXT-FIG. 3.



a, foliage leaf of *A. angulosa*; b, involucre of *A. angulosa*; c, showing internode between involucre and flower of *A. angulosa*; d, foliage leaf of *A. Hepatica*; e and f, involucre of *A. Hepatica*; g, foliage leaf of *Eranthis hyemalis*; h, involucre of *Eranthis hyemalis*.

bracts appear to form a calyx. The bracts have broad leaf-bases, which at their proximal end completely surround the flower-stalk. Each is indented at its apex, the indentations forming three pointed teeth, recalling the bract of *A. fulgens* rather than the lobing of the vegetative leaf (text-fig. 3, e and f).

*A. Hepatica* differs from *A. angulosa* in that the margin of the trilobed leaf is entire, and the bracts, which, as in *A. angulosa* are situated only just below the flower, show no trace of segmentation (text-fig. 3, d, \*; /).

In these species of *Anemone* the bracts or hypsophylls show variations along two distinct lines:—

1- In the position of the hypsophylls.

2- In the proportional development of lamina, petiole, and base, a gradual reduction of petiole and lamina accompanying a broadening of the base.

It is noteworthy that those species in which the hypsophylls show the greatest departure from the segmented leafy type are characterised by a simple vegetative leaf.

Comparing *Ranunculus Ficaria* with the various species of *Anemone*, the vegetative leaf is simple and devoid of any suggestion of lobing or of segmentation. The flower is solitary, and is surrounded by a calyx resembling in appearance the involucre of *A. Hepatica*. Here, however, the calyx lies immediately below the "corolla," no internode between the two being evident.

*EvantUs hyeimlis*. The vegetative leaf consists of three sessile segmented leaflets. The involucre of three bracts is large and resembling the vegetative leaves in size and form. There is, however, no demarcation between involucre and flower, so that here the leafy bract typical of so many species of *Anemone* is combined with the calyx-like position found in *Ranunculus Ficaria* (text-fig. 3, *h*).

#### THE VASCULAR SUPPLY OF THE BRACTS.

The vascular system of *A. japonica* is greatly complicated by the repeated branching of the flower axis. It seemed better, therefore, to consider first of all the form such as *A. nemorosa*, in which the involucre appears to be constant in the number and position of the bracts and in the absence of axillary bracts.

4. *nemorosa*. In the petiole of each of the three bracts there were five vascular bundles—two on the midrib, two laterals, and one basal. As the petiole approached the axis, the laterals divided, one half turning to the outer side, the other half with the lateral remained undivided, the whole bundle passing over to the midrib, which at this stage owing to the fusion, a very characteristic trilobed form was produced.

The petioles meanwhile joined together, thus forming a cylinder completely surrounding the stem. The two marginal bundles diverged widely from the midrib, so that they fused with those of the adjacent bracts and eventually fused with them. Fusion of the laterals and of midribs and laterals, was usually effected at this stage of development (Pl. 21, *a*). The entrance into the main axis, but was occasionally delayed (accessory bundles) which variations were observed, such as the presence of accessory bundles which linked up with the main bundles. Occasionally the marginal bundles occasionally divided, the inner strand receiving the outer strand of

the divided lateral, but eventually fusion with adjacent marginals was achieved and, as before, a ring of six large bundles was formed.

The vascular tissue of the peduncle above the bract node consisted of a single ring of bundles, the number varying between eleven and six. At a general tendency for an alteration of large and small bundles, node the bundles became rearranged, resulting in the formation of gaps in the ring, one being opposite each incoming bundle. Frequently small bundles divided first, the two halves diverging and, in some cases joining the nearest large bundle. The large bundles either divided or swung to one side, leaving a gap for the bract bundle. There were now groups of stem bundles, but fusion between them at this stage was rare.

The usual course taken by the six incoming bundles was as follows. Three midribs passed into the ring and continued down the peduncle as main bundles. Two of the marginals did likewise, while the third passed to one side and joined a midrib, carrying with it the intervening stem bundle (PL 21,6). Occasionally one of the midribs swung across to join a marginal in which case all three marginals passed down as main bundles. In the process a small strand from an incoming bundle was in some cases given off to join a stem bundle.

Meanwhile, the bundles of each of the six groups approached each other more closely, and a certain amount of division and fusion took place. A small strand consisting of two or three xylem elements was occasionally cut off from one of the group bundles, and passed a little way into the pit. This small strand persisted for a short time, but eventually passed out again into the ring slightly to one side of its original position and joined the group bundle.

The group bundles now separated into two, or sometimes three, irregular masses. These began to turn outwards, approaching each other closely at first that occasionally it became impossible to define the contact between each. From this point, as the bundles diverged, a single "contact bundle" frequently proceeded as a small independent bundle and continued down the stem. Presumably it was formed of elements derived from each of the diverging bundles. Each of these joined the nearest incoming bundle. Fusion between stem and bract bundles was not always completed, in some cases the stem bundles formed a subsidiary strand of the peduncle.

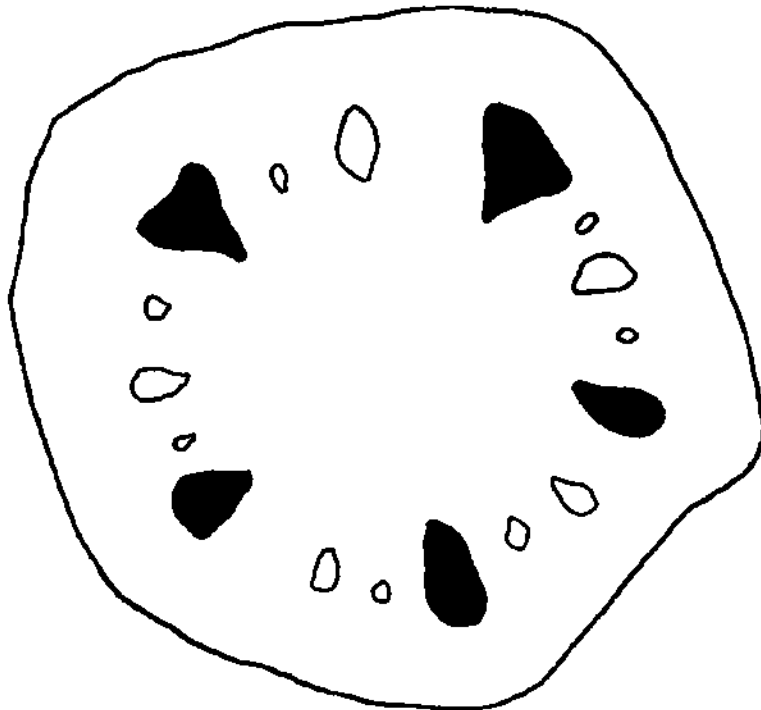
Thus the vascular ring of the peduncle below the node consisted of five main bundles, each of these later on passing out into the bracts, and a number of smaller bundles in groups of one, two, or three, alternating with the main strands. These small bundles might arise (a) as contact bundles, (b) as strands given off from the main bundles when the process of fusion between main bundle and group bundle was completed, (c) as stem bundles which failed to fuse with the incoming bundles (text-fig. 4).

The principal characteristics of the bract bundles of *A. nemorosa* were:—

- (1) Well-developed midrib, which passed straight into the peduncle.
- (2) Division of lateral strands, one half joining the midrib, joining the marginal.
- (3) Fusion of marginals of adjacent bracts.
- (4) The bract bundles formed the main bundles of the petiole.

Worsdell (12) records the presence at the bract node, in *A. nemorosa* of several small bundles, which were observed, to pass into the petiole in inverted orientation, and again pass outwards into the stem, a relic of an ancestral « grandifoliolate » condition, characterised by a

TBXT-FIG. 4.



A Bract bundles shown in solid black.

T.S. peduncle of *A. nemorosa* below the bract node.

«ns described here no trace scattered system of bundles. In the specimen elements separated of such bundles has been found. The small bundles» or be from the group bundles can hardly be distinguished. Wed as indicating a «gratified» J. taj in A. coUWO Wosely resembling *J. newiwosa* in the form of *J. apennina* of its vascular supply were A. ajwnnino and *J. blan* was differentiated in JJ. T shoots were present, but no vascular tissue served, these Unking thes «- Small accessory marginals or laterals were observed. The behaviour UP with the main bundles fairly high up in the petiole.



of the marginals showed more variation than in *A. nemorosa*. There was a tendency for the marginal to swing across to the lateral before this divided. When this happened the resulting bundle divided, half joining the midrib, the other half behaving as a normal marginal and fusing with that of the adjacent bract. On the other hand, the whole lateral might join the marginal, in which case half, or even the whole, of this fusion bundle later joined the midrib. With this variation, fusion of bundles was not always completed before entry into the axis (PL 22, a).

In *A. blanda*, in addition to accessory marginals and lateral, a small strand frequently occurred on either side of the midrib and followed a course similar to that of the former strands (PI. 23, a). In the behaviour of the main bract bundles the chief points in which *A. blanda* differed from *A. nemorosa* and *A. apennina* were:—

(1) In the frequent separation of small strands from the marginals, and even from the midribs, which later linked up either with the original bundle or with the one on the other side.

(2) In a decided tendency for the fusion of lateral and marginal strands to be delayed, marginals of adjacent bracts often fusing before receiving the laterals.

In both these species the vascular ring of the axis above the bract node resembled that of *A. nemorosa*, and the rearrangement of bundles proceeded on the same lines (Pis. 22, b, and 23, b). The spreading out of large bundles preparatory to division was a marked feature in *A. blanda*.

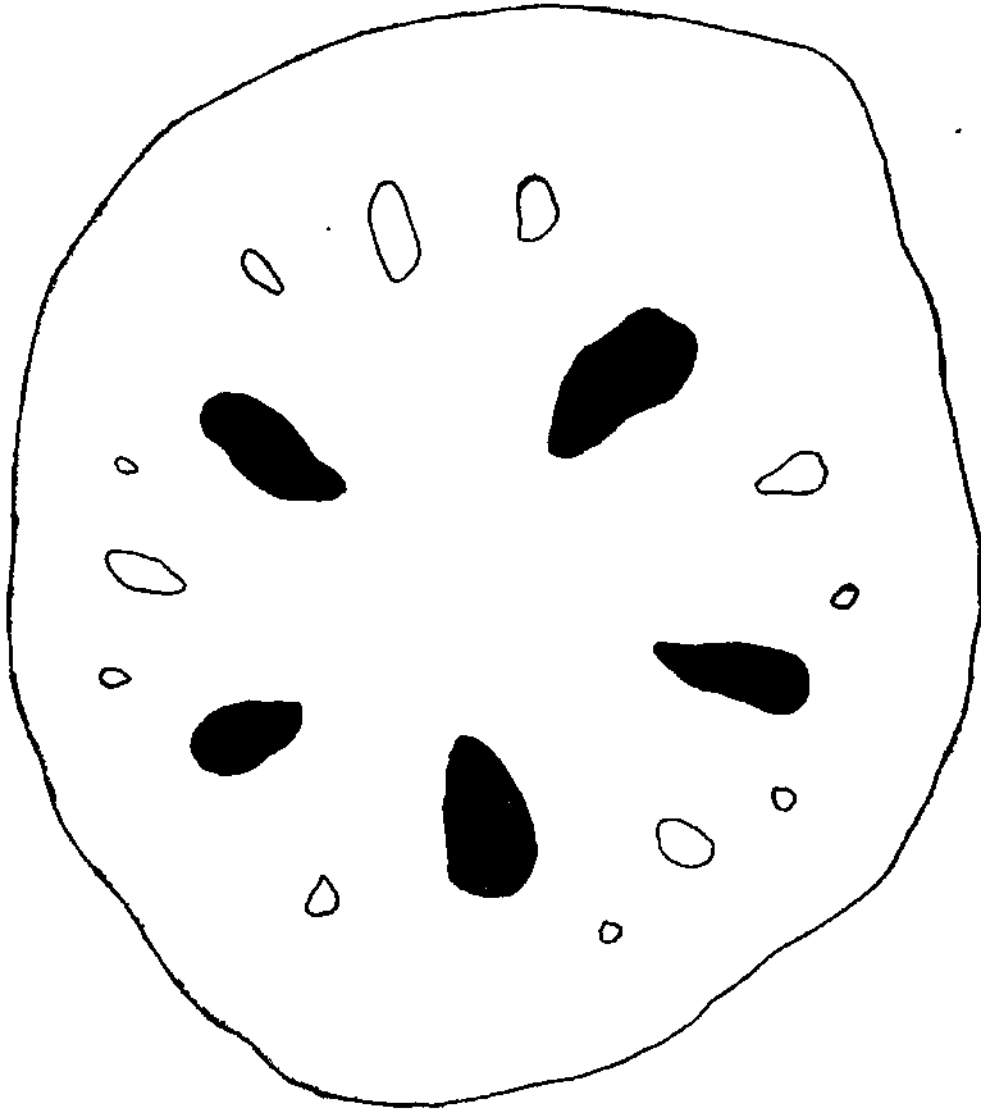
In *A. apennina* four of the incoming bract bundles, two midribs and two marginals, passed into the axis ring and formed main bundles. The fifth might be formed by a swinging across of a marginal to a midrib, or *vice versa*, or both of these might turn in and join, enclosing the intervening stem bundles. Where fusion of marginals had not been completed in the sheathing region of the involucre, it was either accomplished as the bundles entered the axis ring, or failed to take place altogether, the independent marginals joining the group bundles of the ring. These did not differ in any marked degree from those of *A. nemorosa*, dividing and joining the bract bundles in the manner described for that species. During this process also, the separation of one or two xylem elements which passed out again in the course of half-a-dozen sections was observed.

One interesting variation in the behaviour of the incoming bundles was observed in one specimen of *A. blanda*. Here all six bundles passed into the axis ring. One midrib, however, gave off a strand on either side, and gradually became reduced until it could not be distinguished from the stem bundles.

The later course of the bundles in this species showed a very marked difference from that in *A. nemorosa* and *A. apennina*. The stem bundles gave off small strands just as, or just after, they joined the main bundles.

These strands usually joined in pairs and then divided into two or three bundles. The main bundles, after receiving the stem strands, passed inside the vascular ring, forming a second ring, while the small outer bundles became more regular in arrangement (text-fig. 5). The significance of this double ring of bundles will be considered later.

TEXT-FIG. 5.

*A. blanda*. T.S. peduncle below the bract node.

*A. rivularis* and *A. nemorosa* resembled *A. nemorosa* in certain respects, although here, as usual, the petiolar reduction was accompanied by an increase in the number of bundles. In addition to midrib, laterals, and marginals, a varying number of accessory strands were present. Thus in the involucre of a large node of *A. rivularis* there might be as many as six

small accessory marginals on the outer side of the main bundles. The midribs followed the usual course down to the axis, and the laterals generally divided, half joining the midrib and half the marginal (Pis. 24, a, & \* a). The large number of small accessory strands tended to interrupt the regularity of the course of the main bundles, since the former frequently divided and fused among themselves before linking up with the latter, and not uncommonly one or more of the accessory marginal strands remained independently throughout. As in *A. nemorosa*, the laterals did not invariably divide, the whole bundle sometimes joining the midrib.

Divergence of marginals and fusion with those of adjacent bracts was characteristic of *A. sylvestris* and of the larger nodes of *A. rivularis*, where the involucre consisted of three bracts. It was noted that in the latter species, in the axillary shoots which bore only two hypsophylls the marginals tended to remain distinct, even when adjacent accessory marginals joined.

Two nodes of *A. sylvestris* showed features of special interest, in one of which the involucre consisted of four bracts, and from the way in which the bundles linked up it would appear that three of these corresponded to the typical involucre, the fourth being associated with the axillary shoot. The accessory marginals of the bracts on either side of this "extra" hypsophyll diverged and joined, passing in front of the midrib of the latter, but the resulting bundle which would in this way lie directly in front of the incoming bundles of the fourth bract died out, its place being taken by the fourth bract midrib-adjacent marginal on one side of the "extra" bract died out, that on the other persisted as an independent bundle. The two marginals of the fourth bract diverged widely, and, passing behind several bundles of the adjacent bracts, entered the stem as independent strands (PL 26).

The other feature of special interest was the presence of two or three small inverted bundles in each of the three bracts of one specimen. The usual five main bundles were present, and these small inverted strands formed an inner arc. The course of the inverted bundles varied. Several were observed to die out, others passed outwards and joined a midrib marginal or lateral bundle (text-fig. 6). Inverted bundles were not observed in the other nodes of *A. sylvestris* that were examined, and the matter requires further investigation.

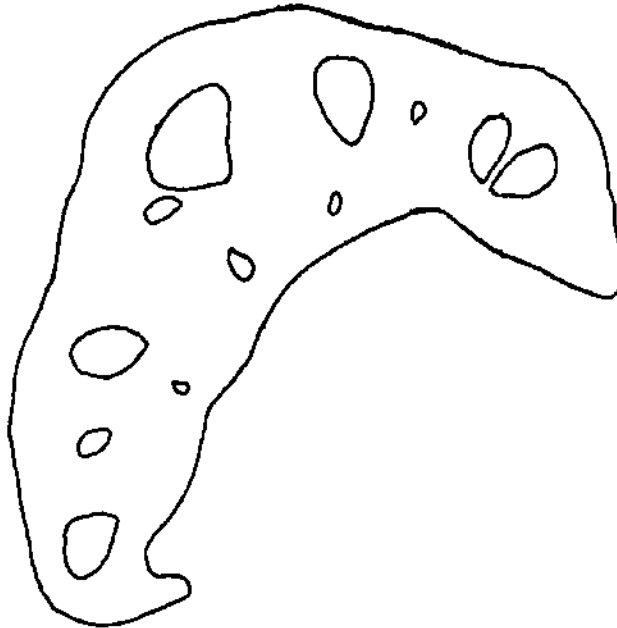
One specimen of *A. sylvestris* exhibited a well-developed axillary shoot bearing an involucre of three bracts, and a flower. At the node of this axillary shoot the entry of the bract bundles into the axis resembled *A. nemorosa* very closely. The vascular ring of the axis, containing thirteen bundles became rearranged in the usual manner, but five gaps were formed instead of six, since the crossing over of a marginal to join a midrib was accomplished before these bundles entered the ring. The five incoming bundles passed down as usual and received strands from stem bundles. In the latter the

fusion of group bundles was much less marked than in *A. nemorosa*, several retaining their identity and constituting subsidiary stem bundles. Contact bands were a characteristic feature.

The larger nodes did not show nearly such a regular course, and exhibited features not present in the smaller node. Gaps were formed in the axis ring, as each midrib entered it usually gave off a strand from either side which passed into the ring before the bulk of the bundle, and eventually joined the stem bundle or group of stem bundles nearest to it. This separation of a small strand during entry into the axis was also observed in the case of marginal bundles (Pl. 24, b).

large node where fusion of bract bundles was completed each of

TBXT-FIO. 6.



*A. tylotm.* T.S. bract petiole showing inverted bundles.

incoming strands passed down as a main bundle. The behaviour of group bundles was markedly irregular. After approaching each other closely in the usual manner, one, two, or three bundles separated out and continued down the axis. In some instances strands were given off to the incoming bundles, but there was not the same out-turning of bundles characteristic of *A. nemorosa* and of the small node of *A. nemorosa*. As a result, small strands from the main bundles assisted in the formation of the smaller bundles of the vascular ring of the peduncle.

A large node where four bracts were present and fusion of bundles was incomplete showed further complications, due to the presence of bundles entering. Of the four midribs, two followed the usual course, a

third, together with the marginal of the adjacent bract and the intervening stem strands, formed another main axis bundle ; the fourth midrib, being carried across by an independent marginal, joined an inturning group of stem bundles and ranked as a main strand. Two marginals also constituted main bundles, and a seventh was later formed entirely from stem strands. The remaining incoming bract bundles were small independent marginals. These joined stem bundles, either entering in the middle of a bundle at one side. In other respects this specimen resembled the one already described. Large incoming bundles gave off a strand at either side, and stem bundles, after joining up, tended to form independent bundles rather than fuse with the main ones.

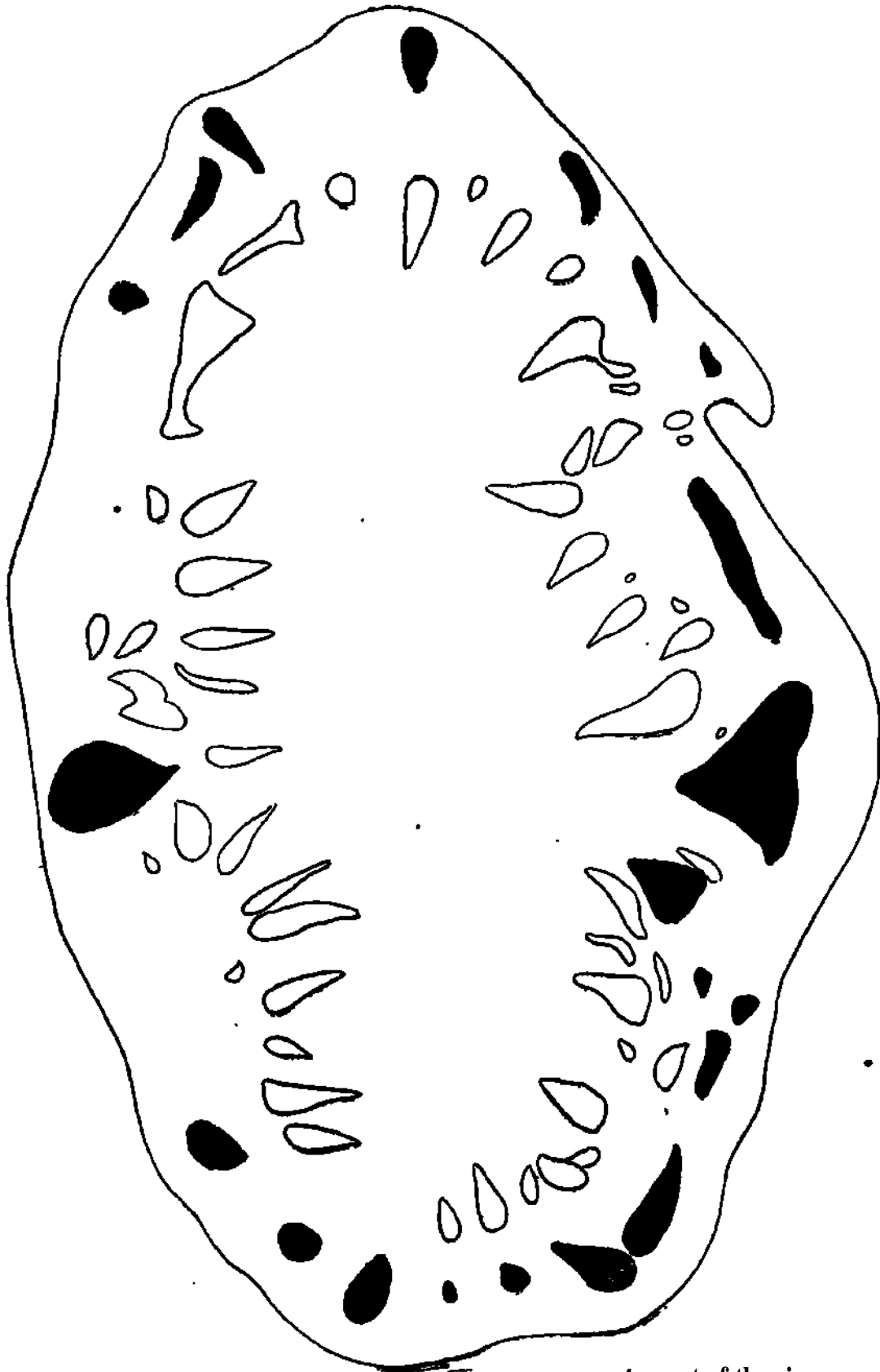
The nodes of the axillary shoots of *A. rivularis* resembled *A. sylvestris* in that all the large incoming bundles as a rule passed down the axis as main strands, and the axis bundles, though occasionally giving off strands to the incoming bundles, usually retained their identity and constituted smaller ring bundles. Thus, as a result, the vascular ring of the axis below the node consisted of a varying number of large bundles, according to the degree of fusion of the bract bundles, and of about twenty small stem strands, frequently arranged in groups of three between the main bundles. Small shoots present in the axils of the bracts of these nodes showed no differentiation of vascular tissue.

The main node of this specimen showed a much more complicated structure than those of the axillary shoots. At the node the first change was the opening of the central ring to receive the vascular bundles of the axillary shoots. During this process the central ring became oval in section and a gap was formed at either end. The curious feature of this rearrangement was that a number of small strands was given off from the bundles between the two gaps, and these, assuming an inverted orientation, passed outside the ring. No suggestion of this was observed in the smaller nodes (Pl. 25, b, and text-fig. 7).

The incoming bract bundles consisted of three midribs, two large marginal bundles, and a group of four small independent marginals which had to link up. Gaps were formed in the irregular axis ring in the usual way except that again small strands became separated and passed out as inverted bundles. The five large bundles entered and continued down the axis, occasionally giving off a small strand to a stem bundle. The four small bundles passed into stem strands and could no longer be distinguished.

During this process the inverted bundles underwent a slight division and fusion among themselves, and gradually assumed normal orientation. About half of these bundles joined ordinary stem strands, but the rest remained independent. As the entry of the large bundles was gradually effected, the stem bundles became arranged in two rings, the outer one consisting of small bundles, while the larger ones formed the inner ring.

TEXT-FIO. 7.

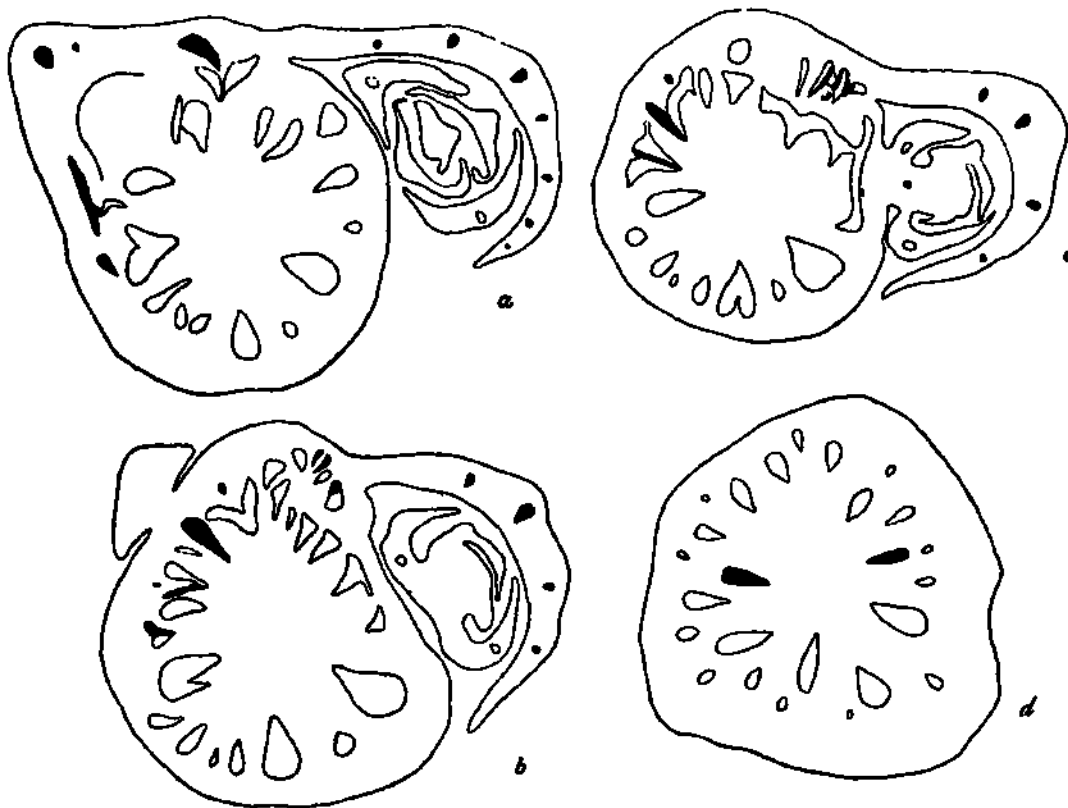


*4. rivularis.* T.8. node showing small bandies passing out of the ring and becoming inverted.

five bract bundles now passed a short distance into the pith, so that <sup>finally</sup> the vascular system of the axis consisted of three rings of bundles, <sup>The</sup> passing into the pith of the large bract bundles to form an inner ring <sup>was</sup> noted, it will be remembered, in *A. blanda* also.

*A. japonica*. Here, as in the other species described, the vascular <sup>supp</sup> of the bracts consisted of midrib, two laterals and two marginals, <sup>and</sup> a varying number of accessory strands, which in this case linked up with <sup>the</sup> large bundles before entering the axis. Typically there were two tracts <sup>a</sup> each node. The two midribs passed down as usual into the stem. <sup>The</sup> laterals divided, but the resulting strands continued to the base of the <sup>ct</sup> bract.

TEXT-FIG. 8.



*A. japonica*. T.S. bract node, *a*, formation of midrib gap and passing out of stem <sup>strands</sup>; *b* & *c*, later stages in the entrance of bract bundles; *d*, below the bract node, showing <sup>the</sup> two midribs in the inner vascular ring. (Bract bundles shown in solid black.)

as independent strands, only joining the midrib or marginal very <sup>occasionally</sup>. The marginals diverged, but fusion or even close approximation of <sup>the</sup> marginals of adjacent bracts was rare (PI. 27).

The vascular ring of the peduncle of a small axillary shoot contain<sup>m</sup> about six or seven large bundles and an equal number of small ones. <sup>Their</sup> arrangement was slightly irregular, giving a suggestion of a double ring. Immediately above the node the bundles began to divide as usual, and, as <sup>H</sup> *4. rivularis*, strands separated and passed out of the ring. Here, however,

There was one important difference. In *A. japonica* none of these bundles were observed to assume an inverted orientation, but remained endarch throughout. Several of the smaller axis bundles were seen to pass out of the ring as entire strands. As a result of this the ring became somewhat irregular, but two definite gaps were formed, one opposite each incoming midrib. These two bundles entered in the manner shown by the species described above, but the remaining bundles, of which there were a number owing to the lack of fusion between marginal and lateral strands, showed variation in their course. Several were joined by bundles which had passed out of the ring or swung across to join these. Others passed into stem bundles, either at the side, at the middle, or dividing between two stem bundles (text-fig. 8)

Some incoming midribs sometimes received strands from the stem bundles, but there was nothing comparable to the very definite division and inturning of stem bundles which characterised *A. nemorosa*, neither did the stem bundles form definite groups, nor tend to lose their identity.

The larger axis bundles, of which there were about seven, including the two midribs, formed an inner vascular ring, smaller ones formed a second, and the very small strands, of which there were several, being a little to the outside, gave the impression of a third ring.

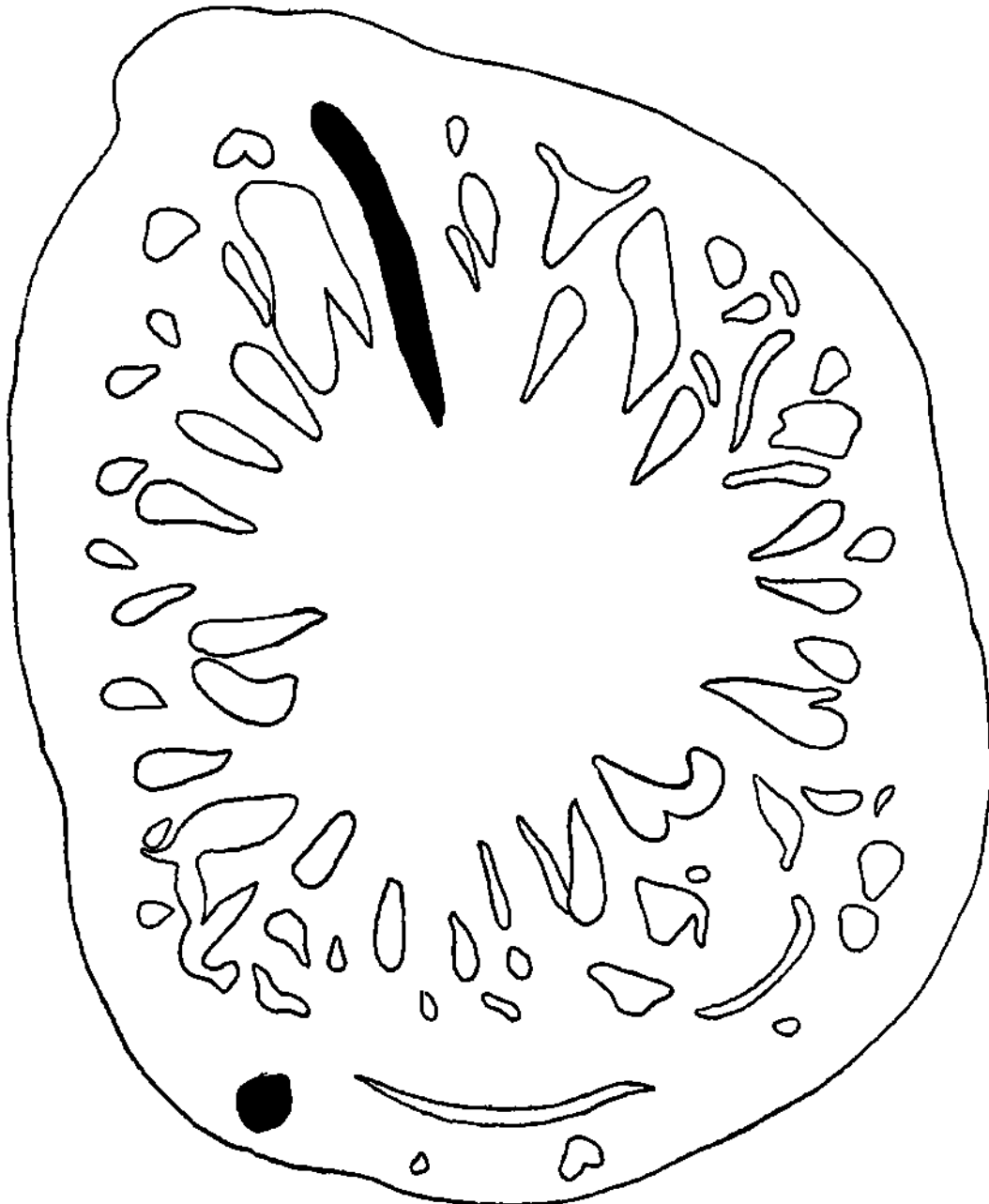
At the larger nodes the vascular cylinder above the involucre consisted of three rings of bundles. At the node the vascular systems of the axillary branches linked up with that of the main axis, giving rise, at this stage, to a very irregularly shaped cylinder. No large gaps were formed opposite the bract bundles, but a separation of strands allowed the midribs to enter and pass into the innermost ring (text-fig. 9). During this process small bundles passed out a short distance from each of the three rings, in the manner described for the smaller nodes. As before, these divided and fused amongst themselves and with the smaller bract bundles, which were now closely approaching the vascular cylinder. Owing to the maze of bundles at this stage it was impossible to trace the later course of the incoming marginals and laterals, and this was done only in the case of the midribs, which continued main axis bundles. As in the smaller nodes, none of the strands which passed out from the axis rings were observed to assume inverted orientation. When the rearrangement was completed the axis exhibited a series of three rings of bundles, the larger ones, two of which were bract midribs, forming the inner ring.

Turning again to the smaller forms which exhibited a definite involucre of three bracts, *A. ranunculoides* as compared with *A. nemorosa* was characterised by a reduction of the bract petiole and a broadening of the base, and showed interesting variations from the latter type (PI. 28, a). Midrib and laterals were well marked in the bract petiole, but the marginals were at this stage represented by a group of two, three, or four



small bundles. Small strands accompanying the midrib and lateral strands occurred, and usually joined the main bundles, but occasionally were observed to continue down as independent strands. The midrib passed down as usual, sometimes giving off small strands. The laterals

TKXT-FIG. 9.



*A.japonica*. T.S. large node. (Bract midrib in solid black.)

divided, and in each case the inner half joined the midrib, but the behaviour of the outer half varied. This bundle frequently remained as an independent strand, receiving contributions from midrib or marginal, but sometimes passed over to join the group of marginals, which linked up to form a main

bundle. As fusion between the marginals was not always complete, small accessory strands might persist. When a lateral strand joined a marginal bundle as a rule divided, the inner half behaving as an independent lateral half as an ordinary marginal. Approximation and fusion of adjacent bracts were accomplished, and were sometimes complete. The division of marginal bundles. In a few instances this division was at right angles to the ordinary plane of division.

The rearrangement at the node differed in several respects from that of *A. nemo*. Stem bundles spread out as in *A. blanda*, but gaps were formed opposite the midribs, before those for the marginals. The small bundles of the Hilary shoots joined the stem bundles on either side of the midrib. Immediately afterwards the large incoming bract bundles blowing the usual course and constituting the five main axis bundles (Pl. 28, A) approached each other closely during this separation of bundles then took place to allow the small bracts to enter. These joined ring bundles, but occasionally an independent lateral continued down as a subsidiary stem bundle. The later arrangement followed the *A. nemorosa* type closely, even to the separation of elements and the formation of contact

*A. coronaria* with a sessile involucre exhibited an increase in the number of accessory bundles and in the degree of independence between these (Pl. 29, a). The midribs followed the usual course; the laterals, which were very large bundles, as a rule divided, but occasionally an entire lateral was observed to swing over to the midrib. The tendency for lateral strands to become independent bundles, which was noted in *A. ranunculoides*, was still more marked in *A. coronaria*. Thus in one specimen the inner half of a lateral bundle, as seen in the figure, came down to the axis instead of joining the midrib; in another an undivided lateral, after giving off a very small branch on either side, behaved similarly, and in several the outer half of a divided lateral was observed to remain independent, although others joined marginals as usual.

The only noteworthy point in the behaviour of the groups of marginals was that the chief marginal sometimes passed into the axis as an independent strand, while the accessory marginals joined those of the adjacent bract. Fusion of adjacent marginals was not always completed, several small bundles often retaining their independence or being separated after fusion.

The vascular ring of the axis consisted of about twelve large bundles, these alternating with one, two, or three smaller ones. Rearrangement proceeded as usual, the midrib gaps being particularly well marked. In their behaviour, the marginal and independent lateral strands showed interesting departures from those of the species previously described. If

fusion of marginals in the involucre base was fairly complete these  
 behaved as usual, two constituting main bundles, the others combining-<sup>^</sup> join  
 a midrib to form a third. If, on the other hand, the marginals failed to j<sup>^</sup>  
 to form a large bundle, two or three independent lateral and m<sup>ar</sup> <sup>o</sup> <sup>l</sup>  
 strands would link up, the resulting bundle ranking as a main stran<sup>d</sup> <sup>^</sup> <sup>^</sup>  
 each example observed, the bracts contributed five main axis bundles,<sup>a</sup>  
*A. nemorosa* (Pl. 29, h). The remaining bract bundles often passed in<sup>to</sup> <sup>the</sup>  
 ring and down as subsidiary bundles, but sometimes were receive<sup>d</sup> <sup>into</sup>  
 the middle ortet on one side of stem bundles.

The groups of stem bundles spread out in the usual manner, <sup>A</sup> <sup>g</sup> <sup>a</sup>  
 role, the central portion of the group continued as a large<sup>^</sup> su<sup>bsidiary</sup>  
 bundle, the outer portions separating to join the large incoming <sup>strands</sup>  
 Two or three small bundles were frequently formed on either side <sup>of</sup> <sup>thes</sup>  
 subsidiary ones by the separation of elements from main or su<sup>bsidiary</sup>  
 bundles.

The bundles now became arranged in three rings, the inner one <sup>co</sup> <sup>n</sup>  
 consisting of five main bundles, a second of the large subsidiary <sup>bu</sup> <sup>ndle</sup>  
 some bracteal in origin, and the third of numerous small bundles in <sup>g</sup> <sup>roups</sup>  
 of two or three.

*A. Pulsatilla.* It was usually possible in *A. Pulsatilla* to distinguish the  
 bract from the bracteoles by reason of its larger size and complicated <sup>vascular</sup>  
 system, the number of accessory bundles being as high as seven <sup>teen</sup>  
 eighteen (Pl. 30, a). The midribs did not exhibit any features of sp<sup>^</sup>  
 interest. Occasionally the laterals divided, sending a strand to the mi<sup>^</sup>  
 and to the marginal; but either of the divided lateral strands might cons<sup>^</sup>  
 an independent bundle. Quite often a lateral failed to divide, the <sup>entire</sup>  
 strand passing down to the axis, and sometimes receiving a strand <sup>from</sup> <sup>a</sup>  
 marginal or midrib. The chief marginal, on the other hand, was <sup>ob</sup> <sup>serve</sup>  
 in several cases to divide, half swinging across to the lateral, half joining <sup>the</sup>  
 subsidiary marginal group. Thus in these latero-marginals the parts p<sup>^</sup>  
 by lateral and marginal were exactly the reverse of those in latero-marg<sup>inals</sup>  
 of the "*nemorosa* type." Fusion of accessory marginals of adjacent <sup>brac</sup>  
 was accomplished, and sometimes this fusion bundle was joined by the <sup>chief</sup>  
 marginal, which at other times remained independent.

In the vascular ring of the axis above the node there were about tw<sup>o</sup> <sup>^</sup> <sup>ive</sup>  
 large bundles and three or four smaller ones. During rearrangement<sup>^</sup>  
 practically, all these bundles divided so that a gap was formed for each <sup>bract</sup>  
 bundle (Pl. 30, b). These incoming strands entered the ring, and almost a<sup>^</sup>  
 of them passed straight down the axis. Very small independent laterals <sup>^</sup>  
 marginals might join stem strands or large bract bundles, but there was <sup>no</sup>  
 linking up of midrib and marginal. No distinction could be drawn between <sup>n</sup>  
 midribs, laterals, and marginals in their behaviour from this point, «&<sup>ch</sup>  
 bract bundle constituting a main axis bundle.

The course of the stem bundles was very characteristic. They formed regular masses between the bract bundles, before dividing into two bundles which diverged and joined the main strands. "Contact strands" were only occasionally formed. In *A. Pulsatilla*, therefore, instead of the ring of five large bundles which has been found to be a constant feature of the peduncle in the majority of species of *Anemone* examined, a ring was formed consisting of a varying number of bundles of approximately equal size, the number depending on that of the incoming bract bundles.

*A. Mjen*\*. The external differentiation into bract and bracteoles was not accompanied by any marked anatomical distinction. Midribs, laterals, and marginals were present as usual, and a few accessory strands. Division of laterals was frequently observed, the resulting strands resembling those of *A. coronaria* and *A. Pulsatilla* in their behaviour, and even showing a marked tendency to remain independent (Pl. 31, a). The accessory marginals ~~linked up with the chief marginals, which diverged and fused with those of~~ adjacent bract. The process of fusion was completed as the bundles were about to enter the axis ring.

The vascular ring of the peduncle consisted of about twelve main bundles alternating with the groups of one, two, or three subsidiary ones. A gap was noted at the node opposite each incoming bundle. Nearly all these bundles entered the ring and continued their course down the axis, but only five main bundles were formed (Pl. 31, 6). These might be formed by midribs and marginals as in *A. nemorosa*, but this was not invariably so. In one case a fusion of a midrib, a marginal, and a lateral to form a main bundle was observed; in another a main bundle was formed entirely by a lateral, while in a third one was formed almost entirely by the linking up of several stem strands, only a very small portion being contributed by bract bundles. In these cases the midrib or marginal, which usually ranked as a main strand, remained as a subsidiary bundle.

Stem bundles formed irregular strands of which turned out to be the bract bundles, while the middle portion continued down as a subsidiary bundle. As in other cases, small strands frequently separated just before or just after fusion with the bract bundles. The five main bundles slightly into the medulla; so that here again a double ring of bundles was formed below the node.

*A. Palmata*. The bract bundles differed from those of *A. fulgens* in their course only. The tendency for the main marginal to remain distinct and contribute to independent lateral strands was a marked feature. The accessory marginals linked up either with the chief marginal themselves to form one fairly large strand. *A. palmata* offered a different type of arrangement, and indeed the smaller ones were far described. The marginals diverged a little, but there was no connection between marginals of adjacent bracts.

The vascular ring above the node consisted of about twelve large bundles alternating with a number of small ones. The first change was the opening of the ring to receive the bundles from the two small axillary shoots which were present. Three well-marked gaps were then formed, one opposite the incoming midrib, which on entering became a main axis bundle (PI. 33, 6). Two marginals also constituted main bundles, and the rest of the bundles passed down as subsidiary strands or joined axis bundles, groups of stem bundles, meanwhile, approached each other and then separated into several strands, some passing over to the bract bundles, but the majority continuing down as subsidiary axis bundles.

*A. angulosa.* The vascular bundles of the small sepal-like bracts consist of midrib, laterals and marginals, and usually two small accessory midribs each bract, which linked up with the midrib or continued down as separate strands (PI. 33, a). The marginals swung across to the laterals, which did not divide. After receiving the marginals, the laterals diverged a little from the midrib, and each entered the axis as an independent bundle. Very rarely the marginals failed to join the laterals, and passed into the peduncle independently.

In the peduncle, above the node, the vascular ring contained from nine to twelve large bundles and several smaller ones. During the rearrangement three gaps were formed, one opposite each incoming midrib, which on entering constituted a main bundle, and shortly after minor gaps appeared opposite the laterals (PI. 33, 6). In one specimen a lateral was seen to form a main axis bundle; but in many cases the lateral divided, two resulting strands diverging and joining the bundles on either side, while in yet other cases the lateral passed over to a ring bundle without dividing. The stem bundles remained distinct except for the fusion required to enclose the incoming laterals. Two stem bundles continued down as main strands bringing the number up to five. Where a lateral became a main bundle only one stem strand ranked as such. The remaining bundles divided and joined the main strands. Occasionally the central portion continued as subsidiary bundle; but true "contact strands" were not formed, as the stem strands usually remained distinct throughout. One of the most striking features of this species when compared with those already described was that the entry of the bract bundles caused far less disturbance of the vascular system of the peduncle.

*A. Hepatica.* In the bracts there was a very close resemblance between the vascular system of this and the previous species. Indeed the only point of difference was that in *A. Hepatica* the marginals were smaller and more insignificant, and might be absent altogether (PL 34, 6).

The axis ring contained about twelve large bundles and several smaller ones, and the rearrangement at the node followed the course described in *A. angulosa*, not differing in any respect except that the division of the laterals after entering the ring took place more frequently (PL 34, 6)-

*Ranunculus Ficaria*. The vascular supply of the sepals consisted of midrib, laterals and marginals, and several accessory bundles which linked up the Main strands (Pl. 35,a). The midribs passed down to the peduncle. The marginals either swung across to the laterals or remained as independent bundles. The laterals diverged slightly and entered the axis, there being no suggestion of fusion of bundles of adjacent sepals. The resemblance between the vascular system of the sepals of *Ranunculus Ficaria* and the bracts of *Anemone* and *A. Hepatica* is obvious.

The rearrangement of the vascular ring of the axis caused by the entry of the petal bundles was not yet fully completed, so that it was represented by about twelve irregularly-arranged strands. The sepal bundles entered between these bundles, and no distinction was observed between the part played by midribs and that by laterals. Almost without exception the sepal bundles divided, the two halves joining the stem bundle on either side. Occasionally an incoming bundle entered at one side or in the middle of an bundle (Pl. 35,6).

The peduncle bundles now linked up to form a vascular ring, consisting usually of five main bundles and several smaller ones.

The specimen examined showed an interesting variation. Here an extra petal bundle occurred in a position similar to that of the bracts of *A. Hepatica*. This "sepal" contributed one bundle to the peduncle, and its course was as follows: — A main axis bundle divided and the sepal bundle entered in the gap formed and continued down the axis without dividing. The two halves of the divided bundle turned into the incoming bundle in the same way that the strands in *A. nemorosa* turned in to join the incoming bract bundles.

In *Anemone nemorosa*. Apart from the presence of a varying number of accessory strands which linked up with the main bundles, the bracts of *Anemone nemorosa* showed a very striking resemblance to the bracts of *A. nemorosa* in the course of their vascular bundles. Midribs, laterals, and marginals behaved in the manner described for that species of *Anemone*. Fusion between marginals of adjacent bracts was completed (Pl. X,a).

Although an internode between perianth and involucre could be distinguished, the vascular strands of the axis had settled down, after the entry of the perianth bundles, into a ring of about four bundles. These divided and moved to one side, leaving the incoming bundles. Each of these entered the ring and continued down the axis. A very characteristic feature of the vascular system of *Anemone nemorosa* is the frequent fusion of the incoming bundles. They usually joined the nearest stem bundle.

The stem bundles remained distinct, and did not contribute in any way to the vascular system. They divided and joined up amongst themselves with the stem bundles. Usually three stem bundles were present between a pair of main bundles.

## DISCUSSION.

From the foregoing account it will be clear that the difference in the form and position of the bracts of these species of *Anemone* is accounted for by well-defined anatomical variations. Certain of these variations in the vascular supply appear to be directly correlated with the form and function of the bracts, since the vascular supply is determined to a certain extent by the physiological requirements of the plant.

The chief interest of the bracts lies in the behaviour of the lateral and marginal bundles. In those species typified by *A. nemorosa* the bundles divide, the outer half swinging across to the marginal, which then fuses with that of the adjacent bract. This is characteristic also of the species *A. sylvestris* and *A. rivularis*, where well-developed axillary shoots normally occur. In *A. japonica* on the other hand, though the laterals divide, there is no fusion either between lateral and midrib, lateral and marginal, or marginals of opposite bracts. This may be correlated with the fact that in this species there is no suggestion of involucre formation, the bracts being simply leaves on the peduncle, in the axils of which shoots arise.

In *A. coronaria*, *A. fulgens*, and species resembling them in the reduction of lamina and petiole, and the broadening of the bract base, there is a decided tendency for laterals and marginals to enter as independent bundles, while in *A. Hepatica* the parts played by lateral and marginal in *A. nemorosa* are completely reversed. Here the marginals swing over to the laterals, which then diverge slightly, but, unlike the marginals of *A. nemorosa*, do not link up with the corresponding bundles of the adjacent bracts. The striking resemblance between the course of the bundles in the bracts of *A. nemorosa* and of *Eranthis hyemalis*, and that between the bract bundles of *A. coronaria* and the sepal bundles of *Ranunculus Ficaria*, needs no further emphasis.

At the bract node the importance of the part played by the marginal bundles in the vascular ring of the axis varies according to the development of the involucral leaves. Of the species examined, *A. japonica* appears to stand apart from the rest in several respects. The bundles of the sessile bracts show little fusion amongst themselves, and rarely with those of the other bract, which arises at the same node, the midrib alone of the incoming bundles constitutes a main axis bundle.

In smaller forms, where branching is restricted or absent and a three-leaved involucre is present, interesting variations in the course of the bundles occur. Where the involucre is indistinguishable from the foliage leaves in size and form (e. g., *A. sylvestris*, *A. nemorosa*) the bracts function as foliage leaves and the vascular supply is of corresponding importance, the bundles being large and dominating the vascular system of the peduncle. The midribs are prominent bundles; the marginals of adjacent bracts link

UP to form bundles of equal importance, and each of these six bundles may constitute a main bundle of the peduncle.

Eduction of petiole and lamina and the broadening of the base to form a more efficient sheathing organ reduces the photosynthetic capacity of the involucre to a certain extent. Bract bundles still form main axis strands; but the bundles of the peduncle take a more prominent part, constituting independent subsidiary bundles in addition to contributing to the main strands. The bracts here take on the more typical characteristics of hypsophylls, showing, for example, a decided tendency to parallel venation, as in *A. coronaria*, *A. Pulsatilla*, and an increase in the number of accessory strands. With the broad bases the linking up of marginal and lateral bundles is carried out to a far less extent than in *A. nemorosa*. The midribs behave as in the latter species; but while fusion between the accessory marginal of adjacent bracts takes place, the laterals tend to remain separate, and division resulting in a large number of small strands, each of which enters the axis as an independent bundle. These modifications are of special interest in view of the "Phyllode Theory" put forward by Arber (i).

In *A. fuigens* and *Ampaimata* the bracts exhibit a still more reduced "Una, and the " hypsophyll characteristics " are more marked. The bract bundles play an important part in the formation of the vascular ring of the axis; but the bundles of the peduncle are not only concerned in the formation of subsidiary strands, but may occasionally form main axis bundles.

In *4. angulosa* and *A. llepatica* the change from a condition in which the vascular system is dominated by that of the involucre to one in which the latter plays a minor part becoming an accomplished fact, and the rearrangement of axis bundles to allow of the entrance bract bundles does not result in a marked disturbance of the vascular ring. The midribs still play an important part; but here the peduncle bundles invariably form one or two of five large bundles, the remaining bract bundles joining the nearest axis strands, either passing in as complete strands or dividing or sending a strand to the axis bundle on either side.

It is only one step further to the condition existing in *Ranunculus Ficaria* which the midribs, laterals, and marginals of the sepals divide and join the axis; Indies, these then linking up to form the five main bundles.

\* comparison of *ErantMs kyemails* with the species of *Anemone* just reviewed with *Ranunculus Ficaria* yields suggestive results. The involucral bracts of *Zranthis hyemali* agree with those of *A. nemorosa* in being similar to the foliage leaves in size and form and presumably in function; but they differ markedly in position being situated immediately beneath the perianth. In the behaviour of the bract bundles of *ErantMs hyemahs* does not differ from that of the bract bundles of *A. nemorosa*, since the strands are



large and assume the part of main strands in the vascular ring of the axis. Thus it would appear that the change observed in the type of vascular system in the various species of *Anemone* is more clearly associated with the change in function of the bracts from that of a foliage leaf to that of a purely protective organ than with the change in position. It may be noted that in one specimen of *Ranunculus Ficaria*, in which an extra leafy sepal was present, the single bundle which entered from this sepal passed down the peduncle as a main bundle, forming a striking contrast to the course usually taken by sepal bundles.

In the majority of species of *Anemone* examined, the peduncle below the bract node exhibits five main strands and a varying number of smaller ones. In many species these bundles form a ring, but in *A. blanda* and *A. f<sup>g</sup>en<sup>s</sup>* the five main bundles pass slightly into the middle, and in *A. japonic<sup>a</sup>*, *A. rivularis*, and *A. coronaria* the bundles form three series, the main bundles constituting the inner ring. Worsdell (12) has recorded the existence of medullary strands and of inverted cortical bundles in some members of the Ranunculaceae, and regards these as relics of a scattered bundle condition which he considers to be the ancestral type not for the Ranales alone but for Angiosperms as a whole.

On this view the ancestral type was of " grandifoliate " habit, the scattered vascular system of the petiole dominating the vascular system of the stem, which would thus be of the scattered bundle type. The change from the " grandifoliate " to the " parvifoliate " habit is believed to have led to a change in the vascular system, the bundles becoming pressed outwards and ultimately arranged in a single ring, while the inverted cortical bundles and the medullary strands remain as persistent vestiges of the outer and inner series.

In one case only among the species of *Anemone* examined have small inverted bract bundles, which might be regarded as traces of a scattered bundle system, been observed (*A. sylvestris*). In the larger nodes of *A. rwulans* small stem strands were seen to separate and to pass out or to ring, assume inverted orientation, and, later, after dividing and fusing among themselves, to re-enter as bundles with normal orientation. A similar phenomenon, but without inversion of orientation, was also noted in *A. jctp<sup>nic</sup>*. The true significance of this process is not clear; but it appears highly improbable that it represents a vestige of an ancestral scattered bundle system, since the bundles which pass out are of peduncle and not of bracteal origin.

With regard to medullary bundles, the evidence obtained in the present investigation is not sufficient to warrant a detailed discussion of Worsdell's theory; but two points may be noted:—

(a) In a case like *A. japonica* or *A. coronaria* where the inner part consists of the main axis strands, the transition from a scattered system of

handles to a ' 1 .  
Ir\* speci wher e ^e single ring is characteristic it is these large bundles  
which form the vascular tissue

(bin dull ar y strands in *Anemone* are not invariably leaf-traces, since  
in *A. fulgens* One \* ^e peduncle bundles was observed to constitute a member  
of the inner ring.

An alt<sup>o</sup>TM\*te exP<sup>lft</sup> nation of medullary bundles has been suggested in the  
case of cert<sup>am</sup> ol(\*ers, ^us<sup>m</sup> Begoniaceae the medullary vascular system  
of cer\*ia<sup>n</sup> species is regarded as a result of the formation of  
tysten<sup>f</sup> an<sup>r</sup>nizo<sup>mes</sup> which increase the demands made on the conducting  
the exV<sup>r</sup> o?lle(\*ting<sup>an</sup>J redistributing reserve material (4). If this were  
the nh<sup>an</sup>atlon \*<sup>n</sup> the case of species of *Anemone*, it is difficult to see why  
jn<sup>r</sup> M<sup>ono</sup> 11)en<sup>o</sup>n should make its appearance in a few species only,  
hract<sup>no</sup>le<sup>18</sup> \*ar<sup>e</sup>> the double ring of bundles might be regarded as a means  
to prevent Overcrow<sup>^</sup>i<sup>ri</sup>g'. This explanation, however, would not hold good  
for A<sup>ll</sup> K<sup>nd</sup>. a an<^ ^'f<sup>ty</sup>ens<sup>9</sup> where the number of bundles is not sufficiently  
large. S<sup>hout</sup> any suggestion of overcrowding. It is hoped that the  
sign: g<sup>o</sup> can<sup>ce</sup> \*<sup>o</sup> this scattered type of vascular system may be indicated by  
further investigation.

The study with<sup>^</sup>ch has been made of the vascular anatomy of the bracts and  
of the bract nodes of these species of *Anemone* appears to support the view  
that the bracts of the calyx of *Ranunculus Ficaria* are homo-  
logous structures. If this were so, then it is conceivable that the bracts of  
&• he<sup>st</sup> r<sup>utu</sup> res> also h<sup>pat</sup> a an(\* \*^e ca<sup>y</sup> of species of *Ranunculus* other than *Ficaria* may  
be homologous.

realising that in many cases part of the so-called " perianth " of  
flowers may arise by the sterilisation of stamens, it is considered that the  
results obtained in the present investigation support the view expressed by  
Goebel (3) aU(\* ^ ^ra<sup>ntl</sup> (6) that bracts may also take part in the develop-  
ment of the perianth so that this structure may in one flower have two distinct  
the jointly different origins. There appear to be no real grounds for limiting  
it the development of petaloidy to any one set of organs of the flower axis, and  
it seems probable that a part of the perianth, the original function of which  
would be at least partly that of protection, may be of bractal origin.

SUMMARY.

1. The form and position of the bracts of various species of *Anemone* are described and these are compared with the bracts of *Eranthis hyemalis* and the sepals of *Ranunculus Ficaria*.
2. A detailed account is given of the vascular supply of the bracts of the flowers of *Anemone* and of the part played by the bract bundles on entering the flower axis.

3. Where no definite involucre is formed (*A. japonica*), there is little fusion between the bract bundles, and on entering the axis ring, only the midrib forms a main bundle. In species resembling *A. nemorosa* with a leafy involucre the characteristic features are :—

(a) Division of lateral bundles, one half joining the midrib, the other half swinging over to the marginal.

(b) Fusion of marginals of adjacent bracts so that in all six bundles enter the axis.

(c) The vascular ring on the axis below the node consists of five bundles, all of bracteal origin, and of several smaller ones.

Species with an involucre of sessile bracts with reduced lamina at the base (*A. coronaria*, *A. fulgens*) show a tendency to parallel venation; increase in the number of bract bundles, lack of fusion between lateral and marginal; but the vascular system of the axis is still dominated by the involucre.

In *A. angulosa* and *A. Hepatica*, where the reduction of the laminae in involucreal leaves results in a calyx-like structure, there is no fusion of marginals of adjacent bracts; the part played by lateral and marginal in *A. nemorosa* is completely reversed—although the midribs still become main axis strands, the entry of the bract bundles causes relatively little displacement of the axis ring, and peduncle bundles become main strands, while bundles from the bracts show a tendency to divide.

4. The course of the sepal bundles of *Ranunculus Ficaria* resembles the bract bundles of *A. Hepatica* very closely; but here all the entering the axis ring play a subsidiary part, and as a rule divide.

5. The vascular supply of the bracts of *Eranthis hibernalis* resembles that of *A. nemorosa* in all essentials.

6. The variations in vascular anatomy are considered in relation to the difference in function of the bracts.

7. The significance of the double ring of bundles which occurs in some species of *Anemone* is discussed; but the evidence obtained in this investigation is regarded as insufficient to be in any way conclusive.

8. The vascular anatomy of the bracts and the bract node of these species of *Anemone* appears to support the view of the homology of the marginal of *A. Hepatica* and the calyx of *Ranunculus Ficaria*.

I wish to express my thanks to Dr. H. S. Holden, who suggested this investigation, and both to him and to Miss Bexon, for their kindly help and criticism.

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- J2. <sup>—</sup> <sup>—</sup> A Study of the Vascular System in certain Orders of the Ranales. *Ann. of Botany*, vol. xxii. 1908, pp. 651-(582, pis. 32 & 33.

## EXPLANATION OF THE PLATES.

## PLATE 21.

- <sup>a</sup> <sup>a</sup> *nemorosa*. *a*, the course of the vascular bundles of the bract; *b*, the course of bract and Peduncle bundles at the node. In this and the succeeding diagrams the midribs are shown in heavy red, laterals light red, marginals broken red, accessory bundles broken black, peduncle bundles black.

## PLATE 22.

- <sup>a</sup> <sup>a</sup> *Pennim*. *a*, vascular bundles of the bracts; *b*, of the bract node.

## PLATE 23.

- <sup>a</sup> <sup>b</sup> *«nda*. *a*, vascular bundles of the bracts; *b*, of the bract node.

## PLATE 24.

- <sup>a</sup> *tylvestim*. *a*, vascular bundles of the bracts (*x*, inverted bundles); *b*, of the bract node.

## PLATE 25.

- <sup>A</sup> *«Kdaris*. *a*, vascular bundles of the bract; *b*, of the bract node (\*, bundles which pass out of the ring, assume inverted orientation, and later, assuming normal orientation, re-enter).

## PLATE 26.

- <sup>a</sup> *tyheatim*. Vascular bundles of bracts of four-leaved involucre.

## PLATE 27.

- <sup>A</sup> *J«ponica*. Vascular bundles of bract.

PLATE 28.

*A. ranunculoides.* *a*, vascular bundles of the bracts; *b*, of the bract node (*x*, bundles from axillary shoot).

PLATE 29.

*A. coronaria.* *a*, vascular bundles of the bracts; *b*, of the bract node.

PLATE 30.

*A. Pulsatilla.* *a*, vascular bundles of the bracts; *b*, of the bract node.

PLATE 31.

*A. ftdgens.* *a*, vascular bundles of the bracts; *b<sub>t</sub>* of the bract node.

PLATE 32.

*A. palmata.* *a*, vascular bundles of the bracts; *b*, of the bract node (#, bundles of axillary shoots).

PLATE 33.

*A. angulosa,* *a*, vascular bundles of the bracts; *b<sub>g</sub>* of the bract node.

PLATE 34.

*A. Hepatica.* *a*, vascular bundles of the bracts; *b*, of the bract node.

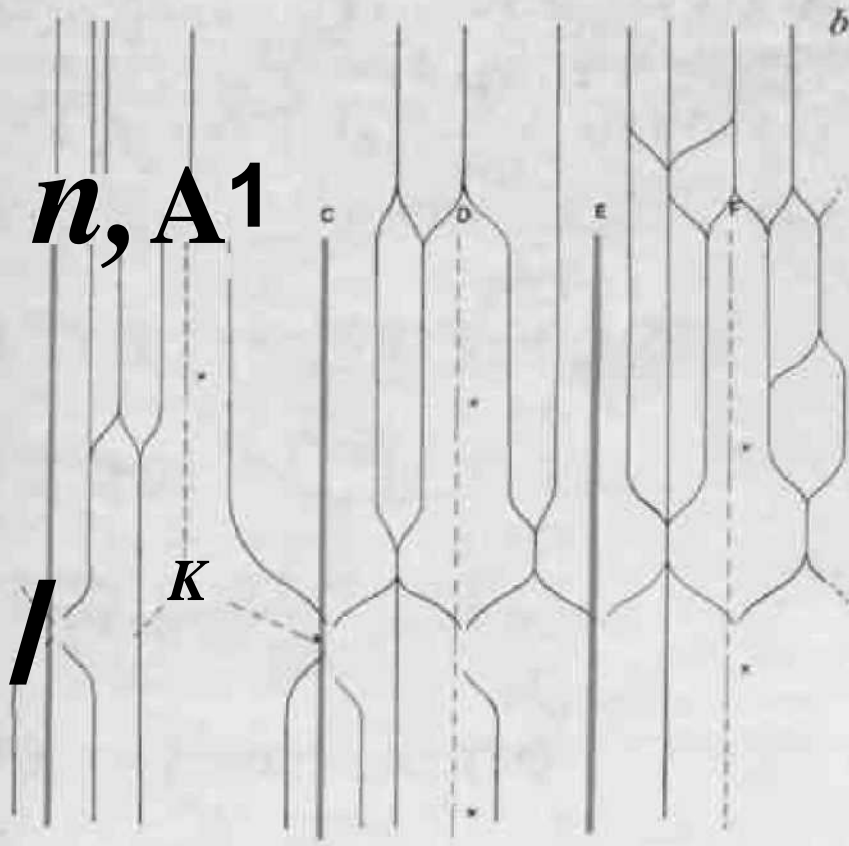
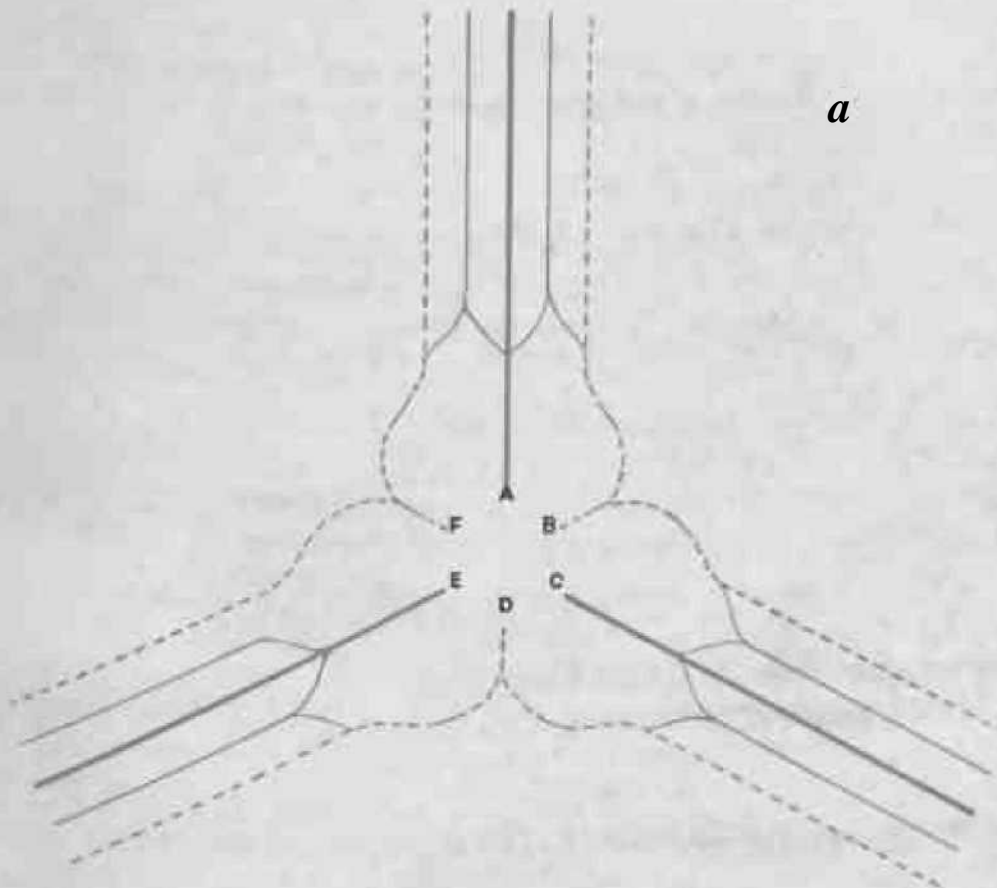
PLATE 35.

*Ranunculus Ficaria.* *a*, vascular bundles of the sepals; *6*, of the sepal node.

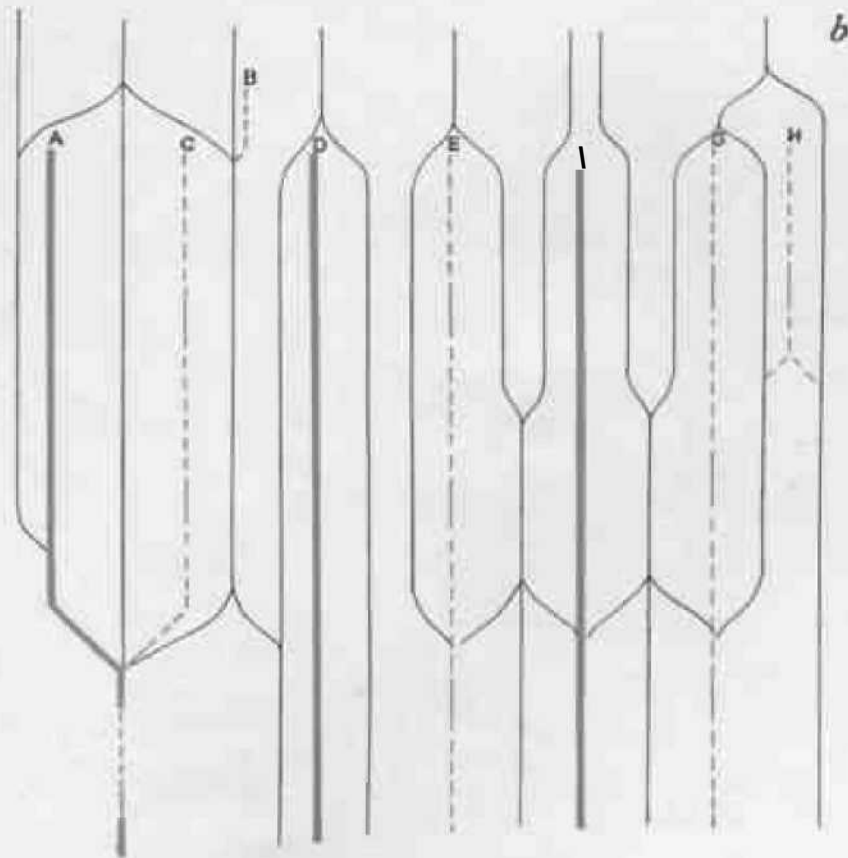
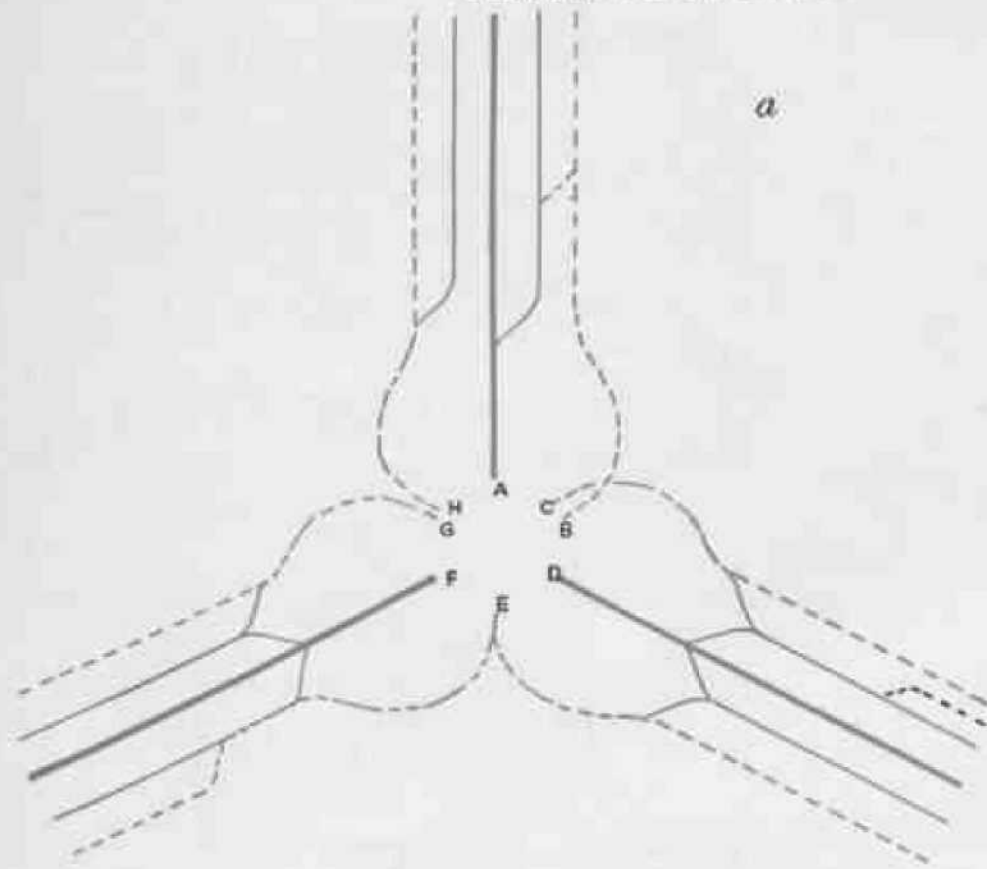
PLATE 36.

*Eranthis hyemalis.* *a*, vascular bundles of the bracts; *6*, of the bract node.

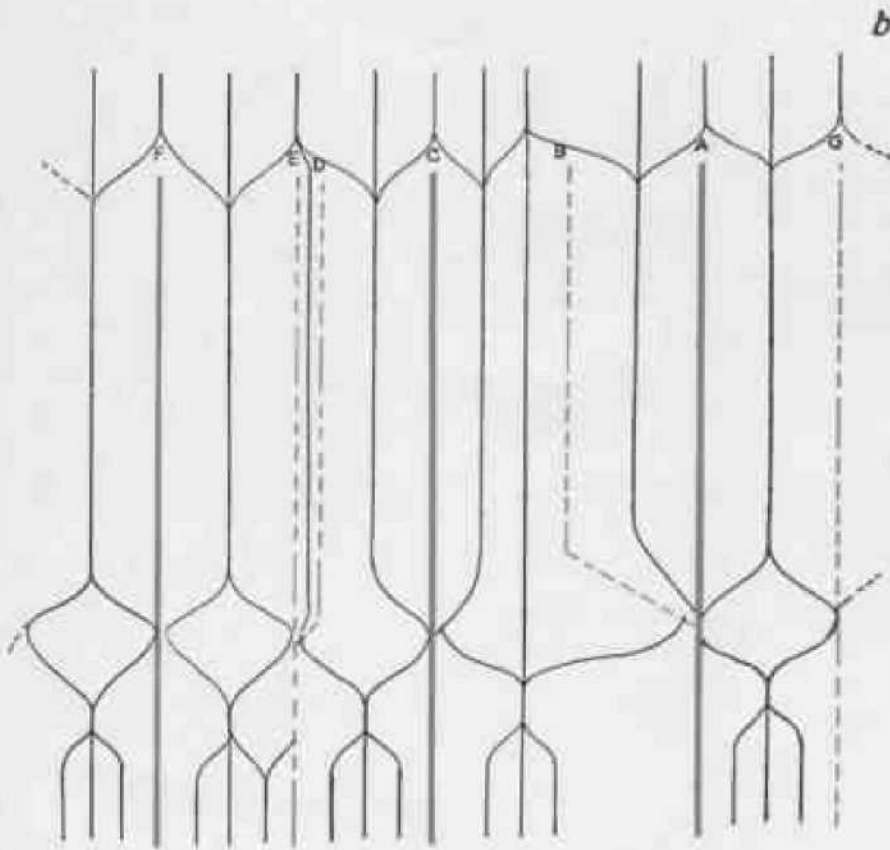
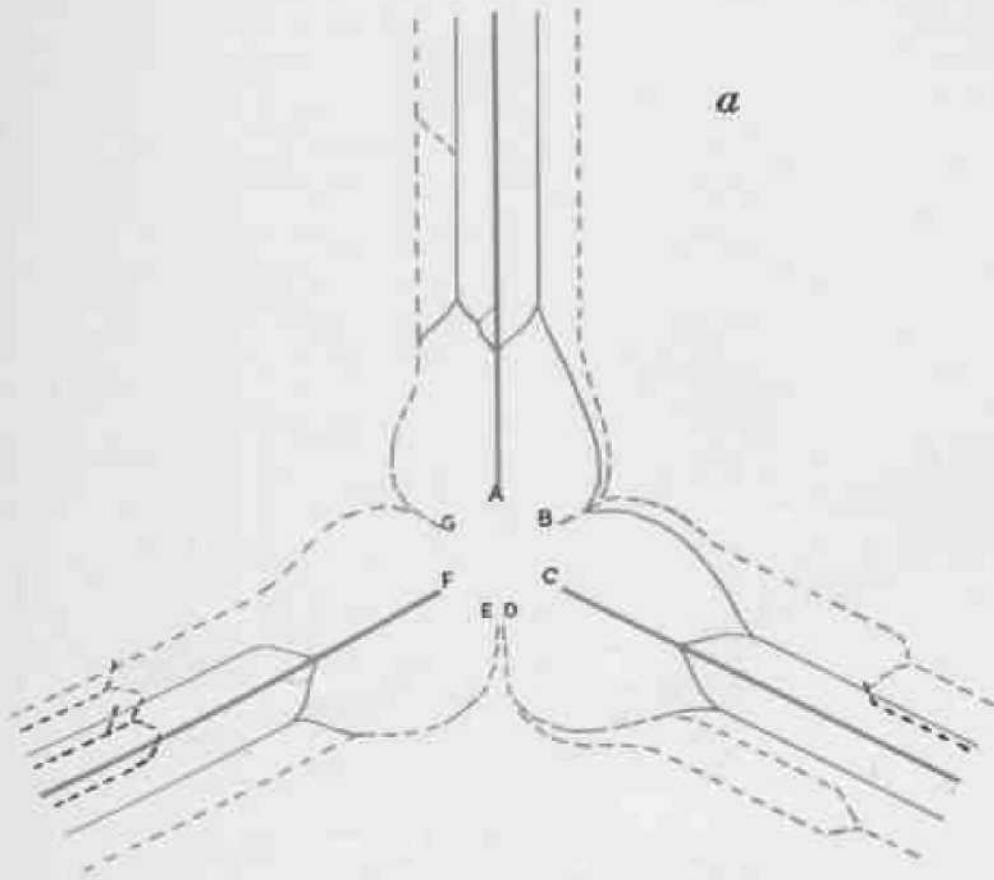
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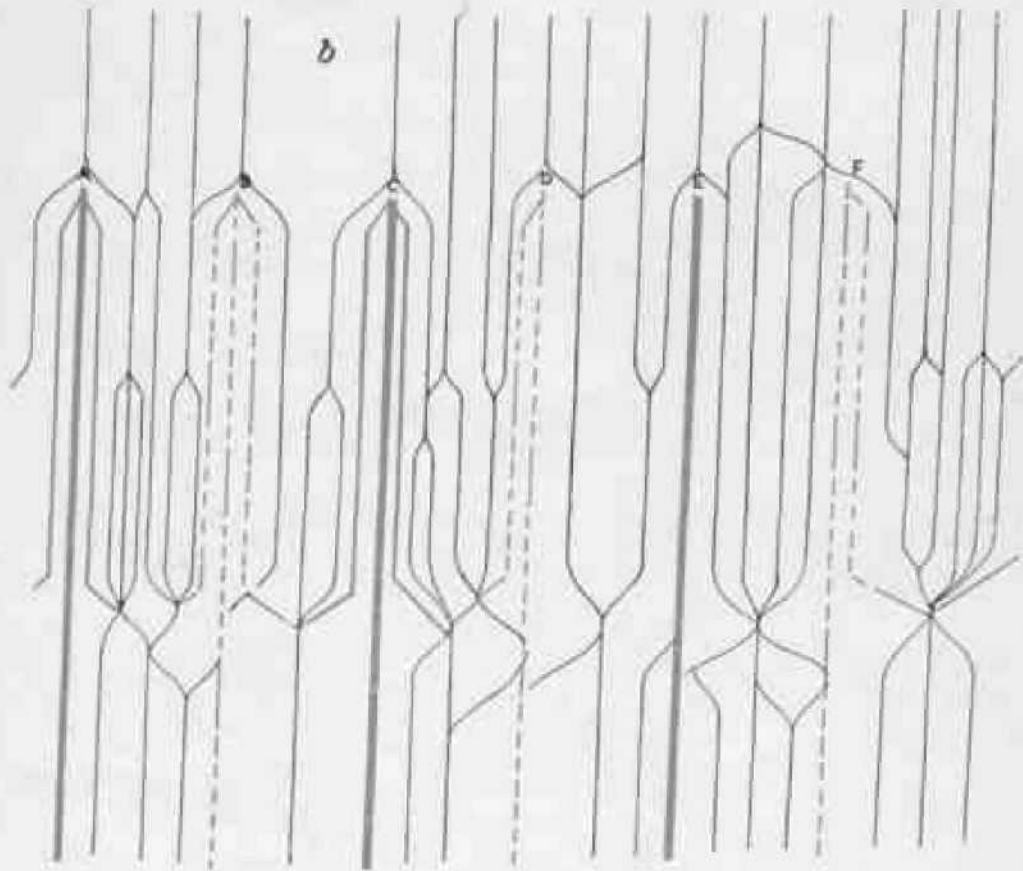
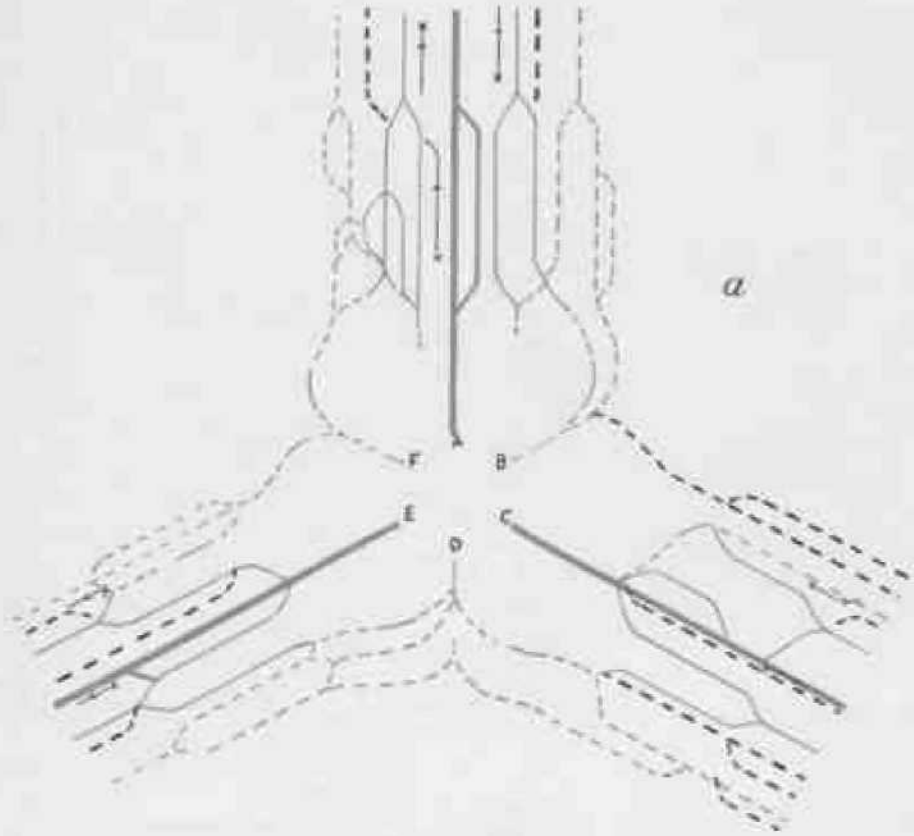
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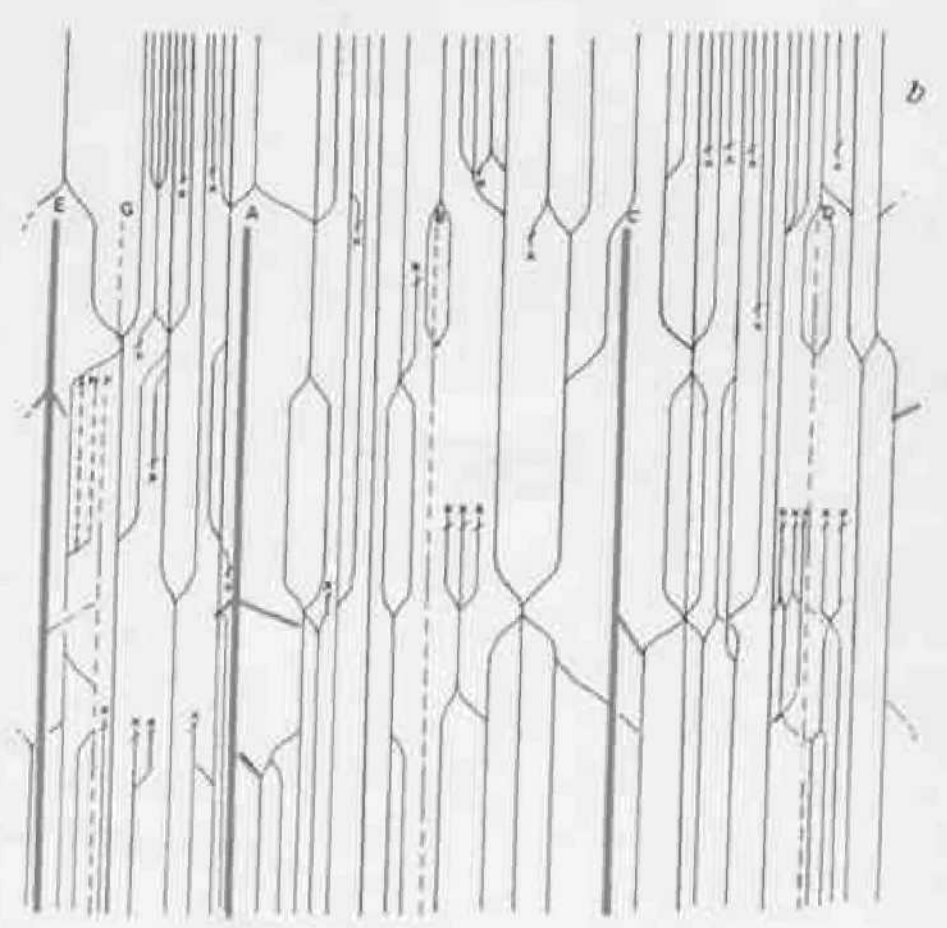
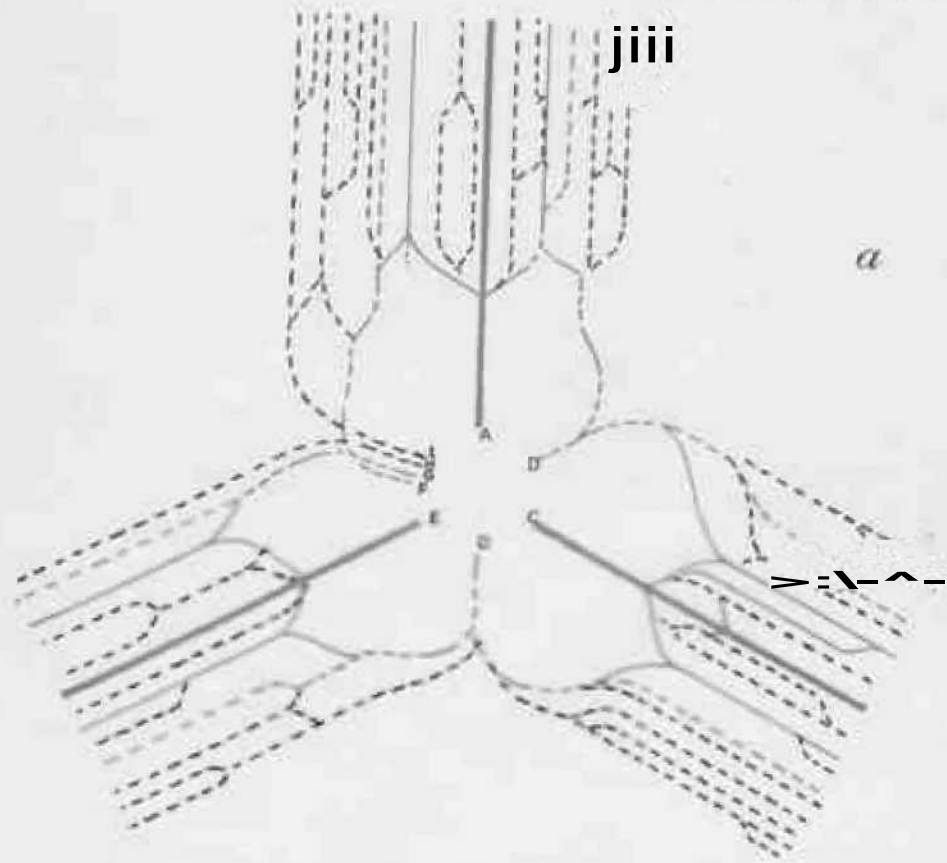
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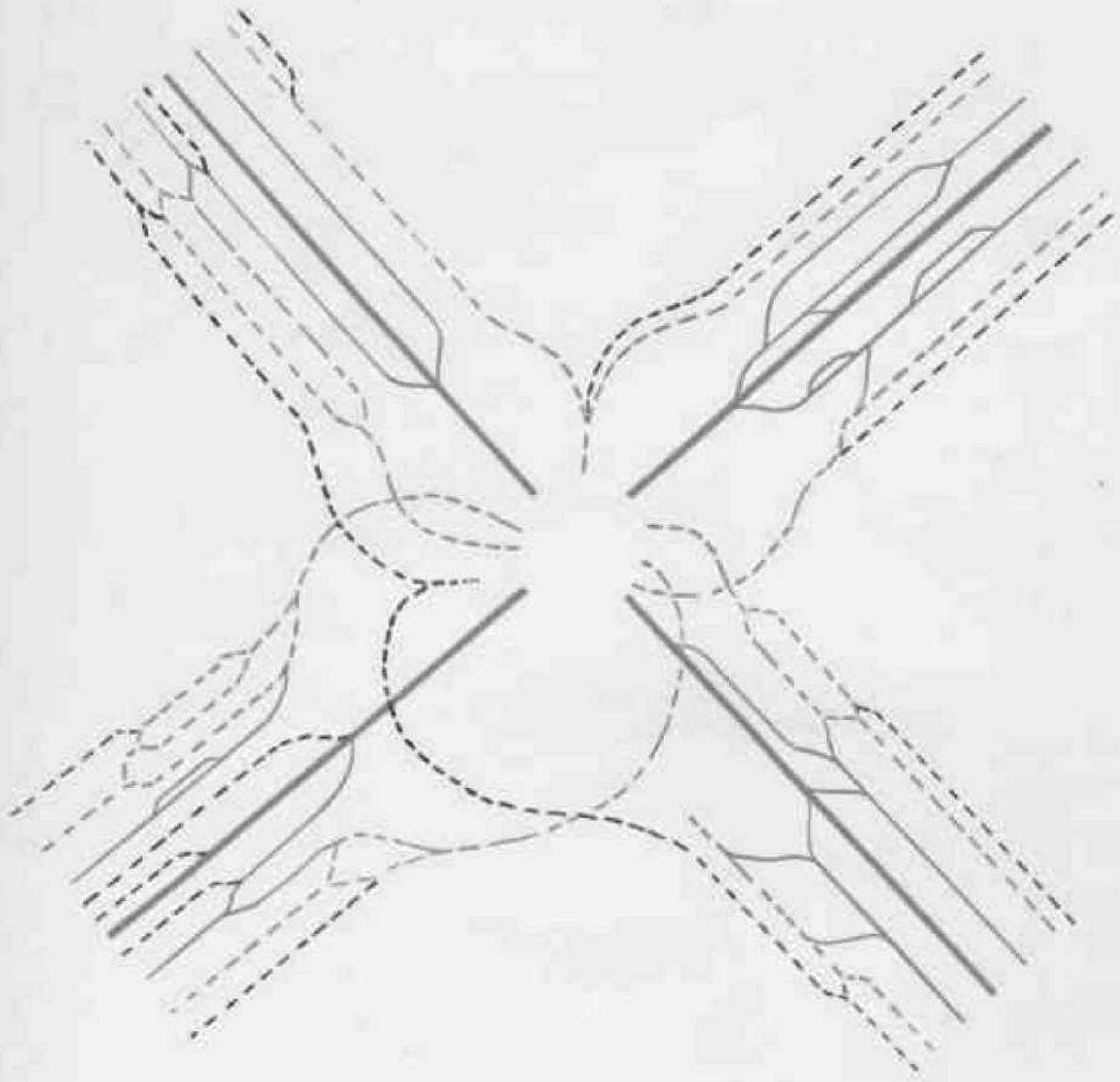




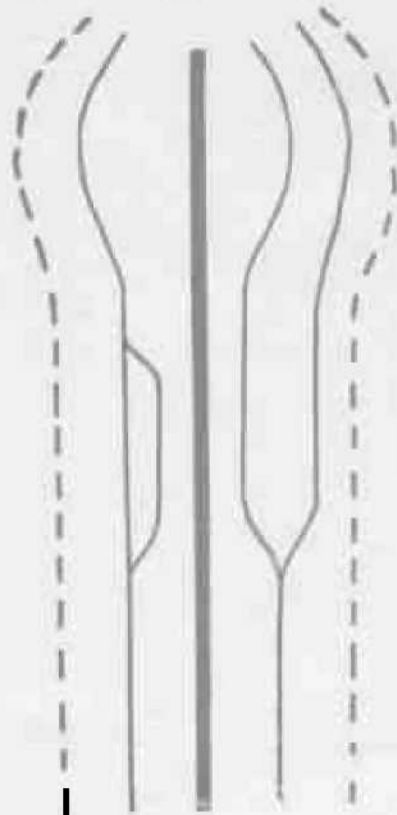
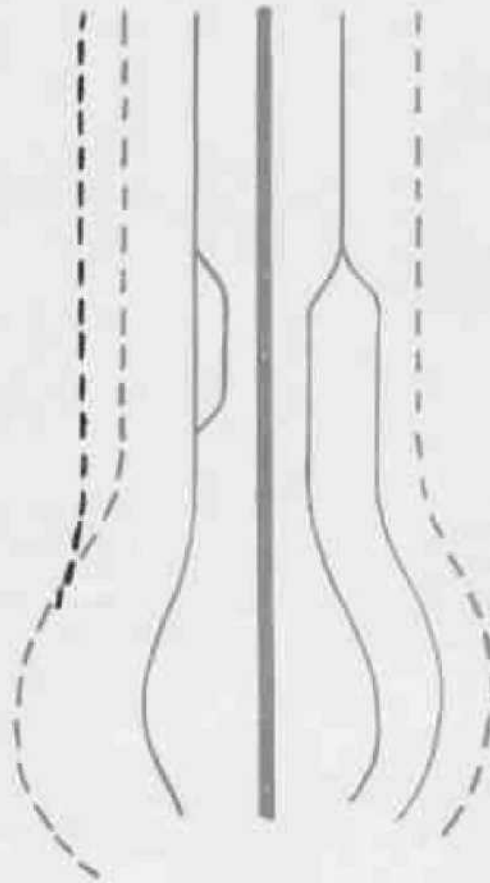
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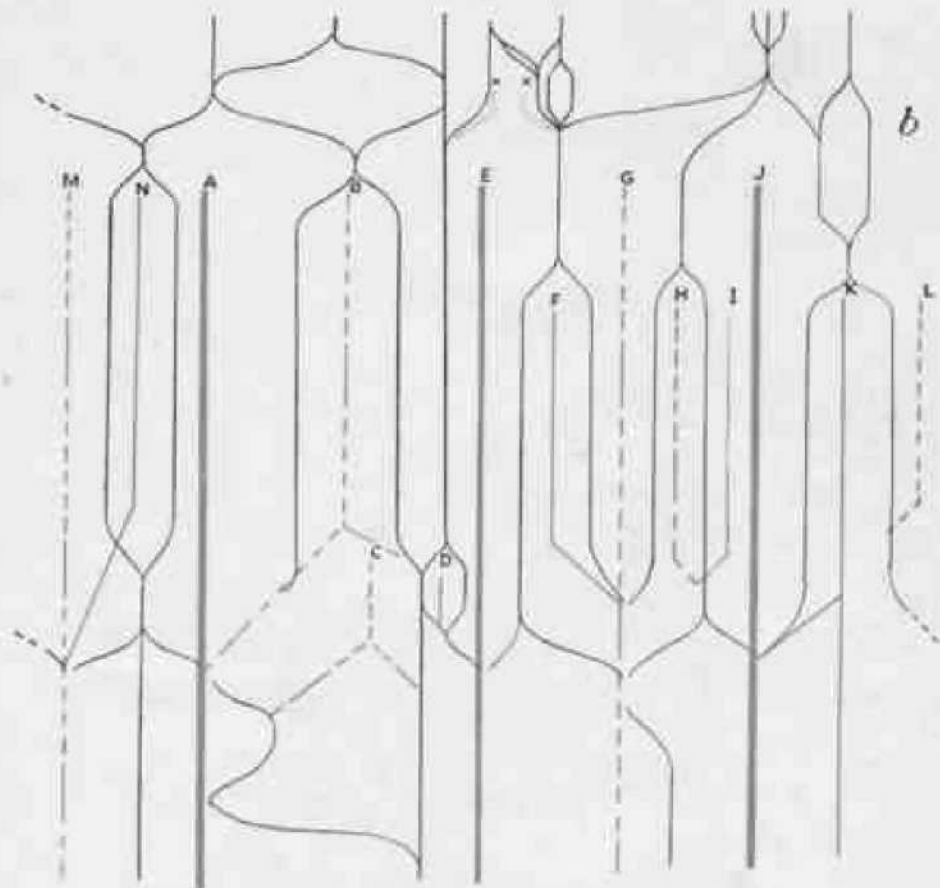
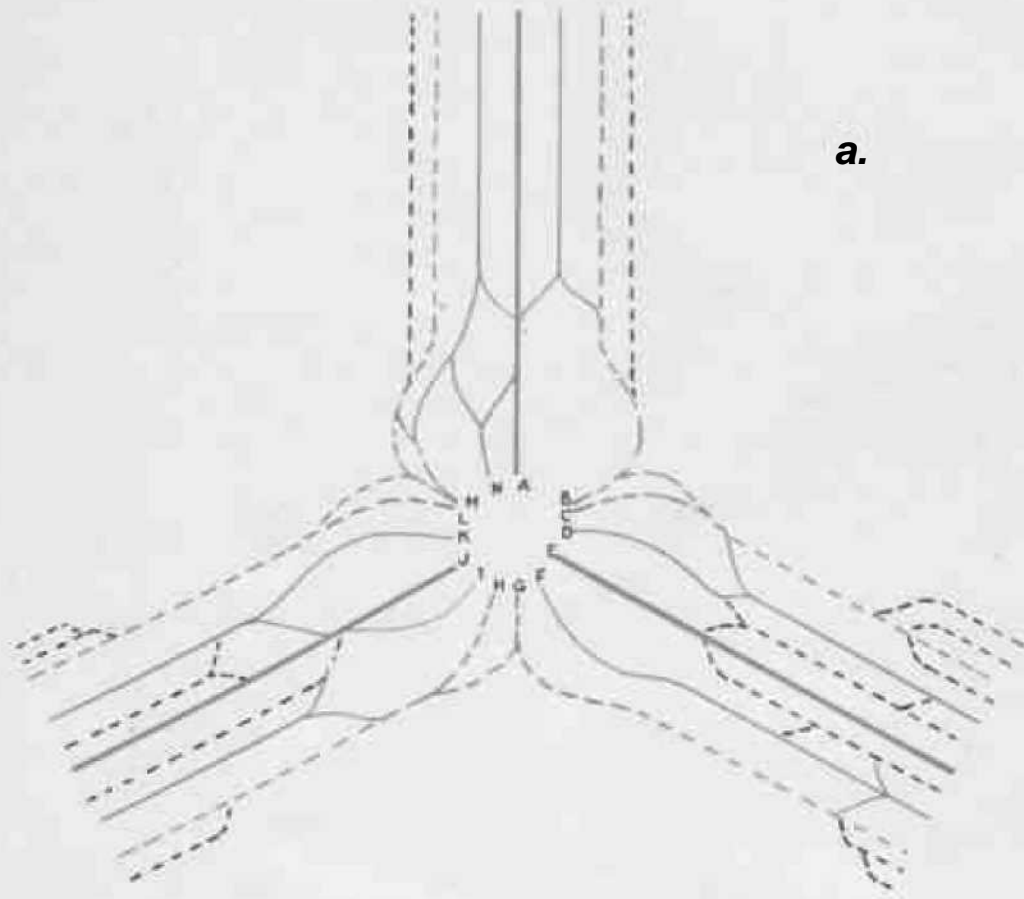
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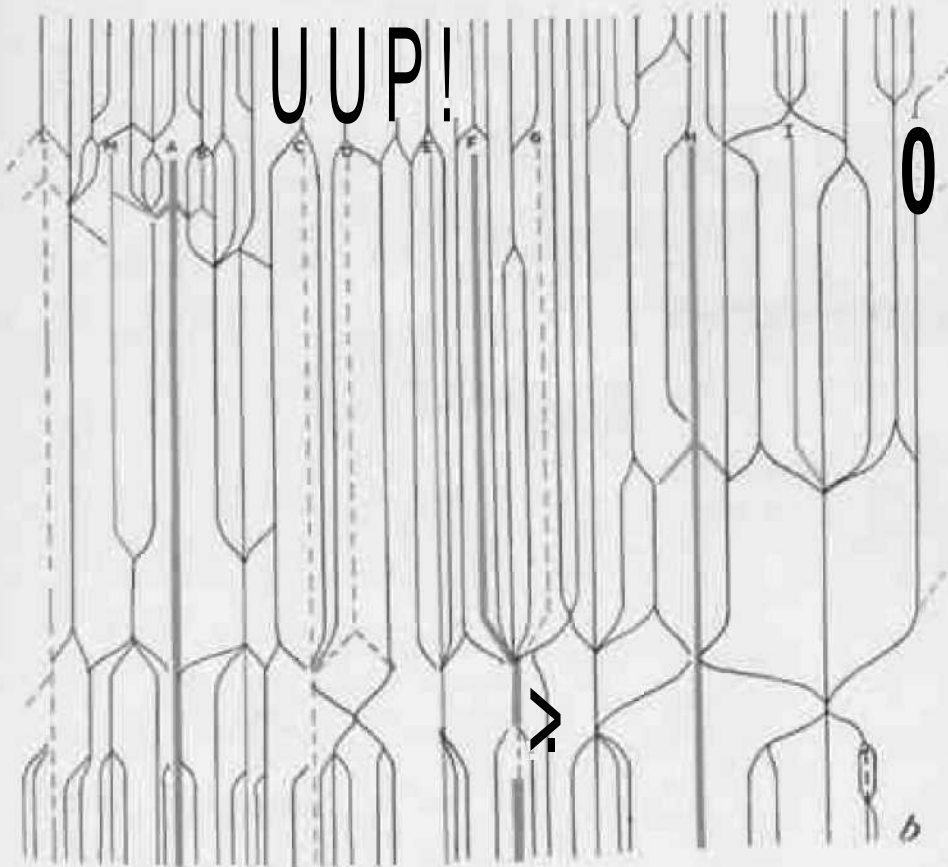
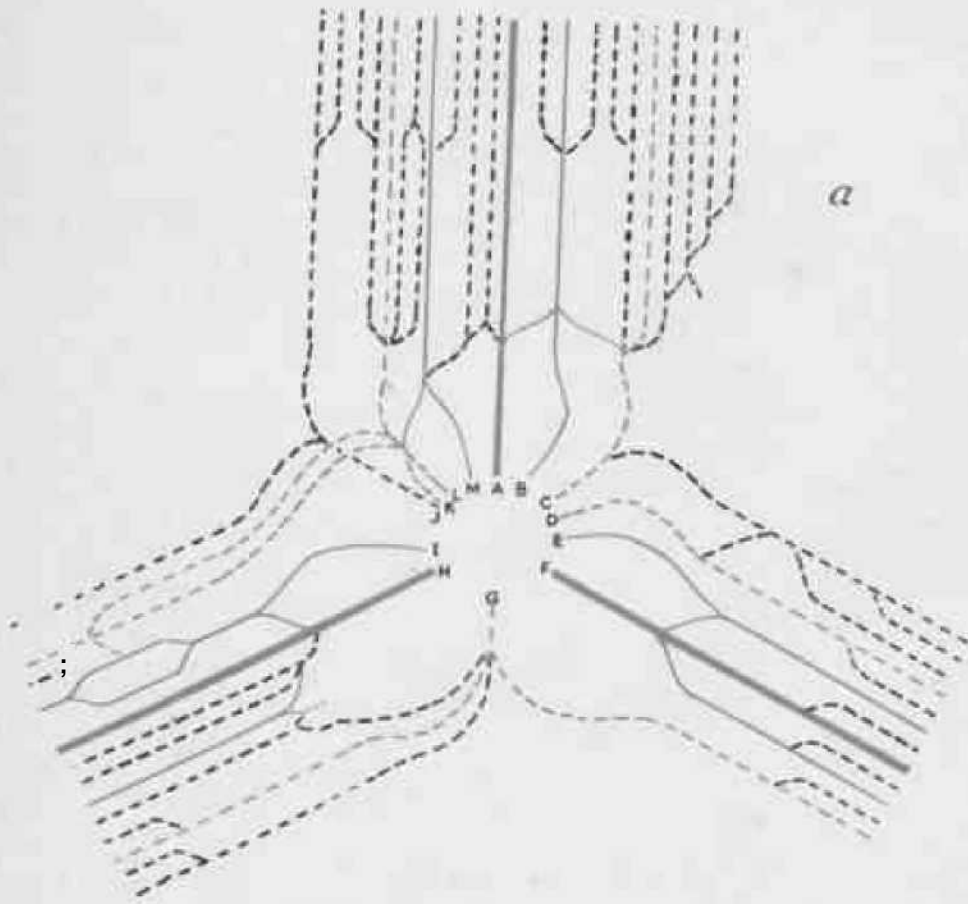
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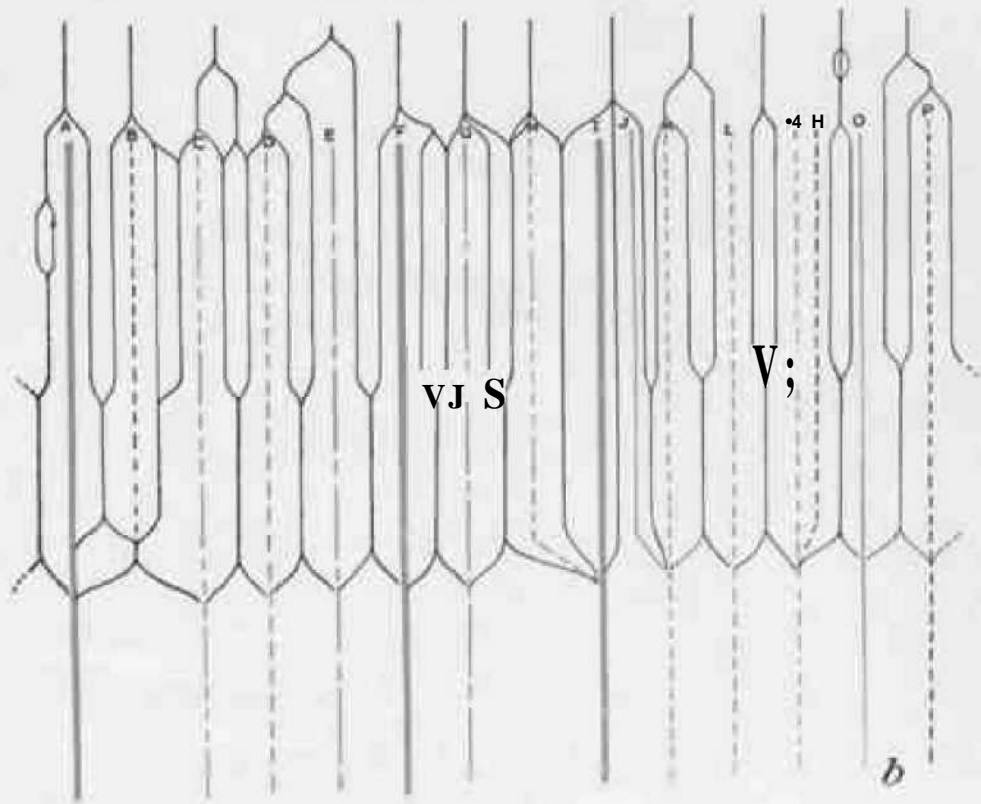
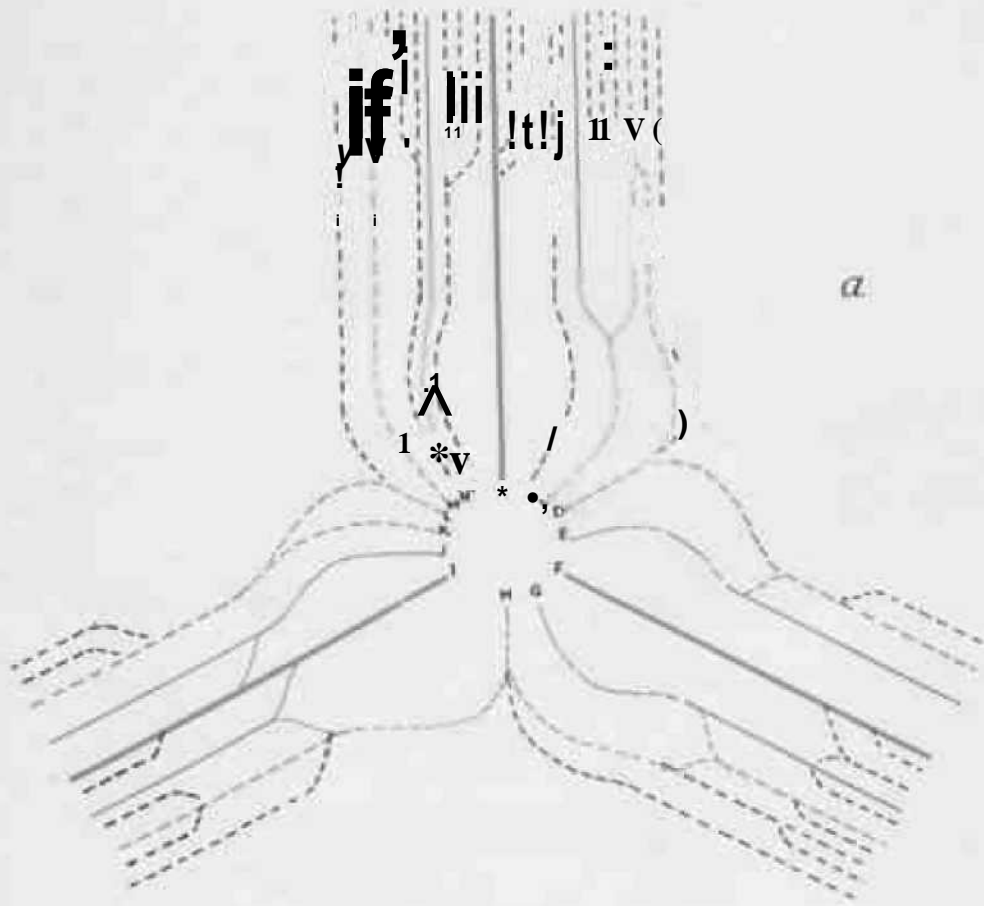
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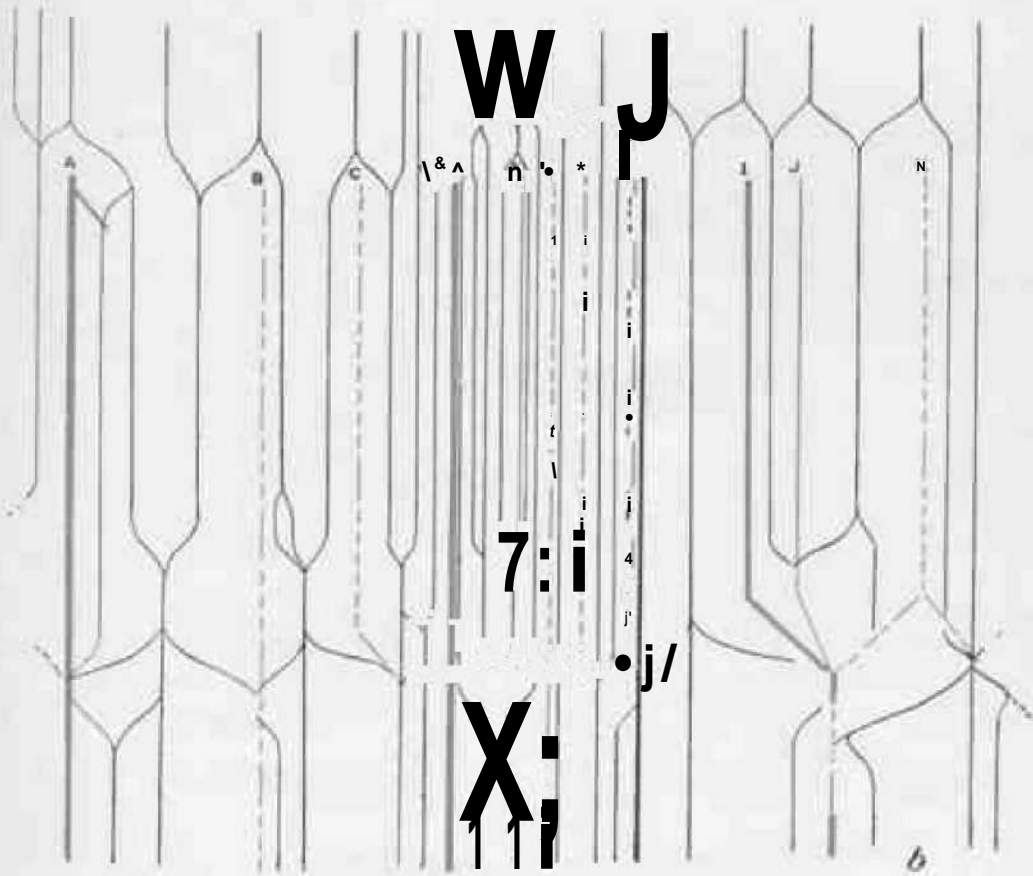
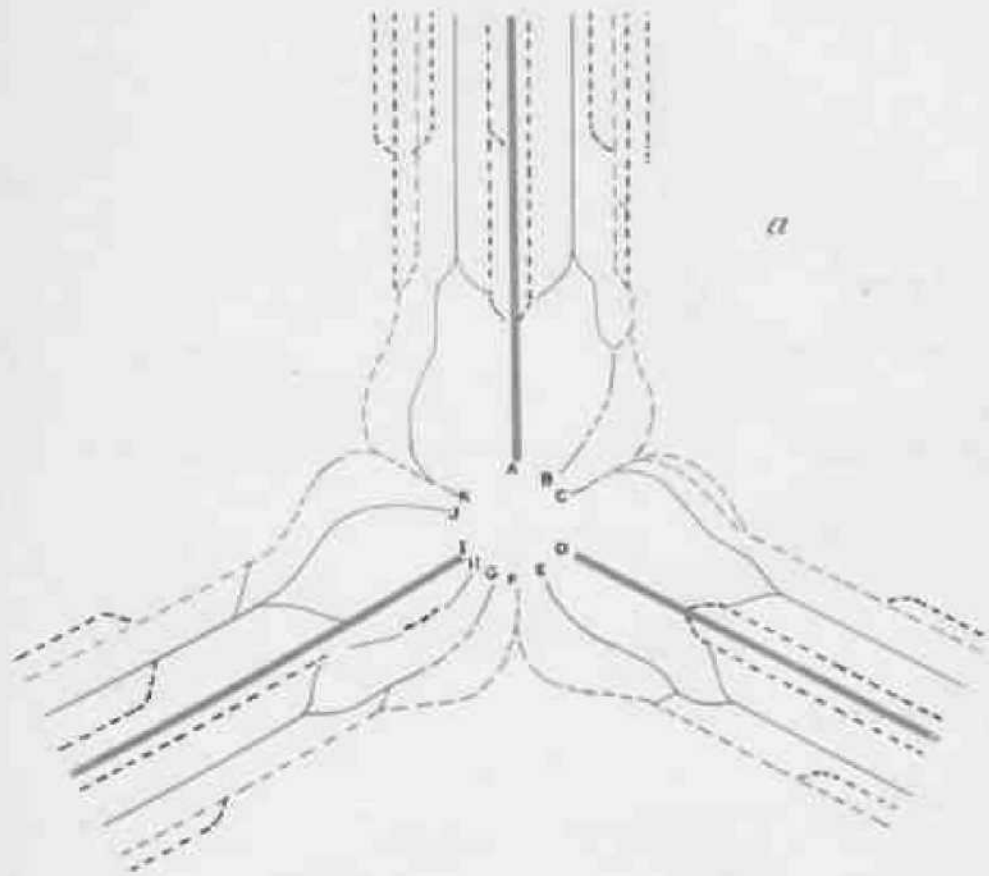
**AtTEMONE RANUSCULOIDES,**



А5ЕК0КЕ СОКОСАРИА.

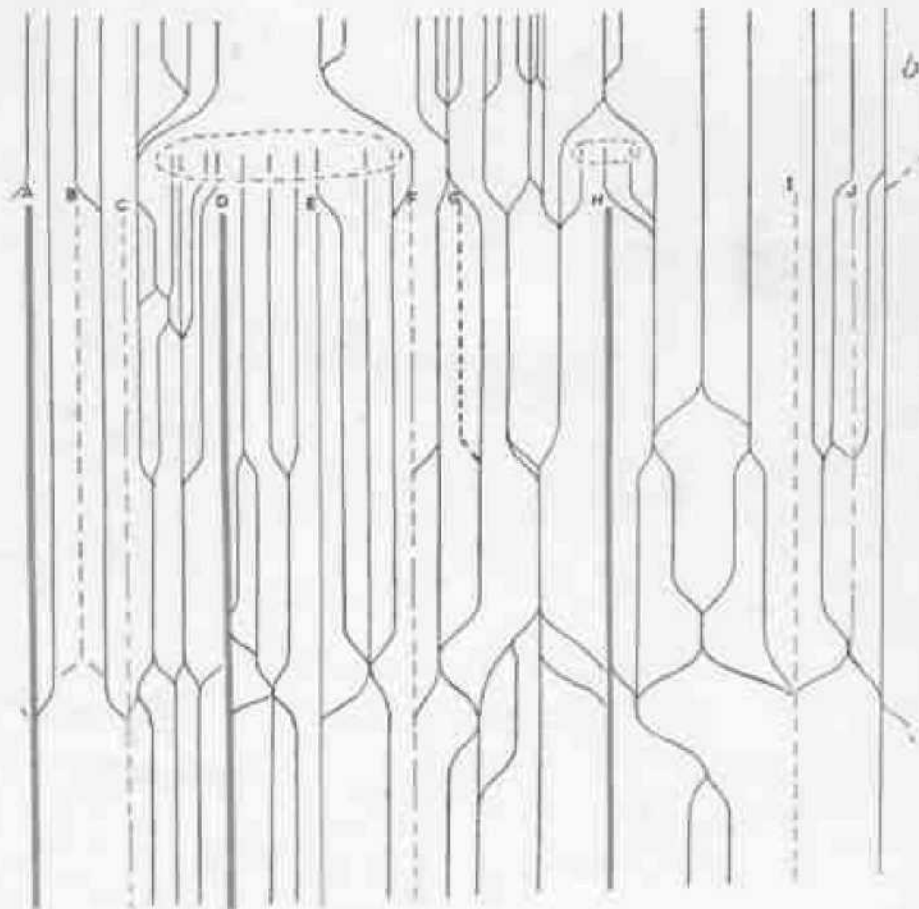
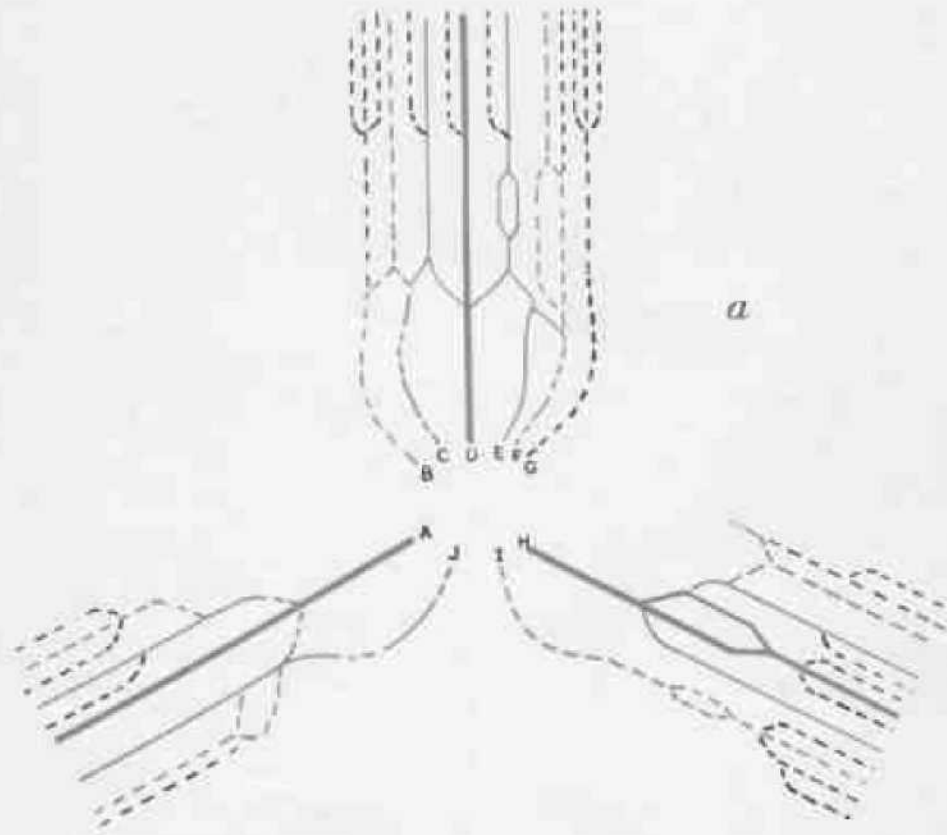


ANEMONE PULSATEJA,

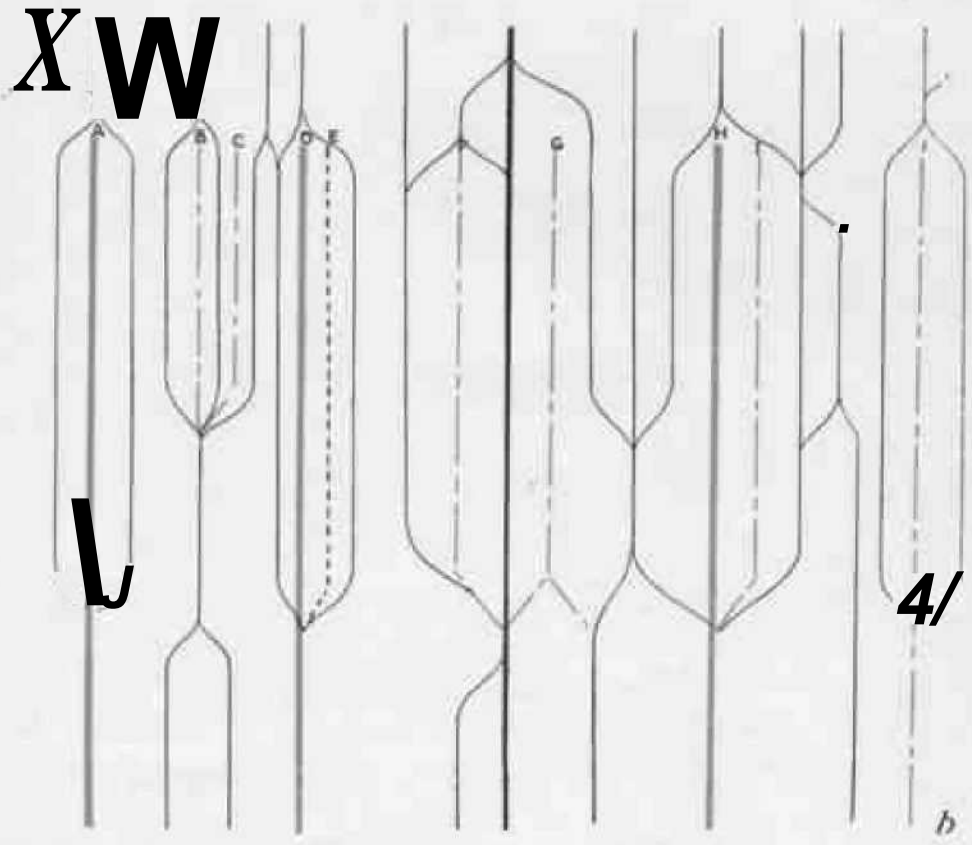
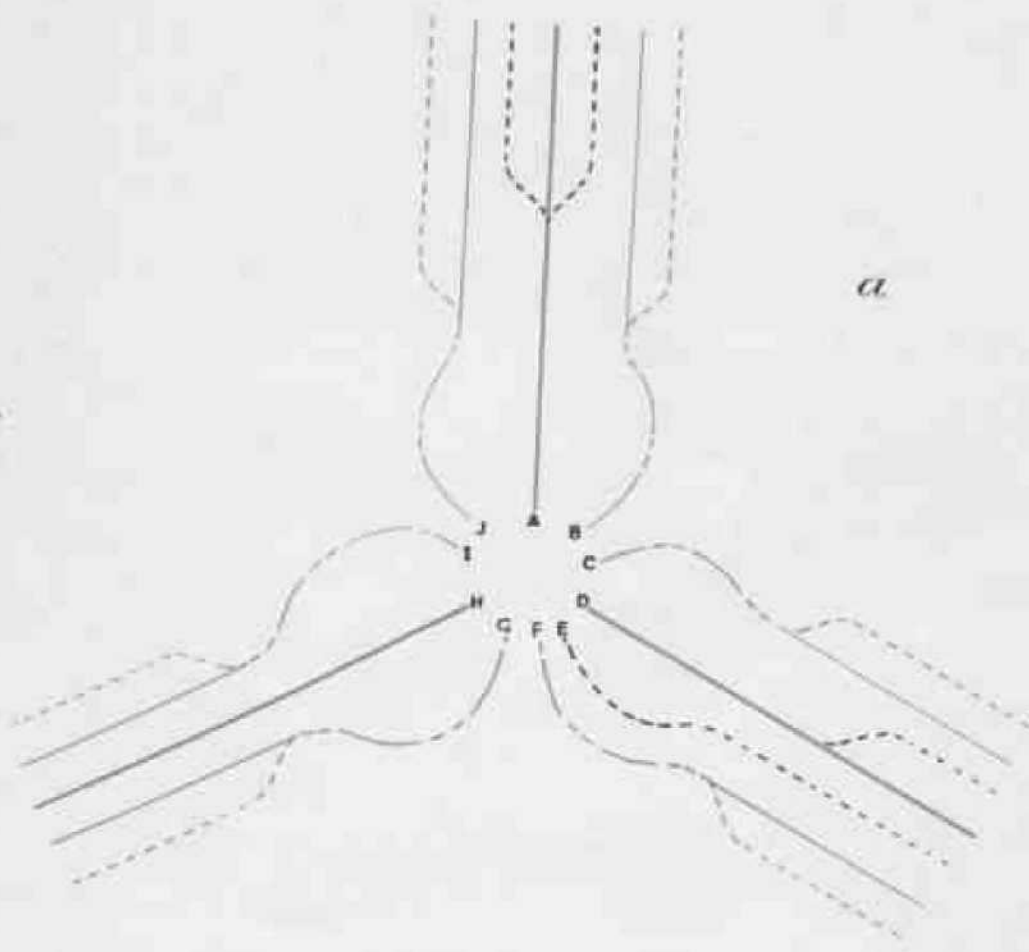


ANEMONE FULOEN3.

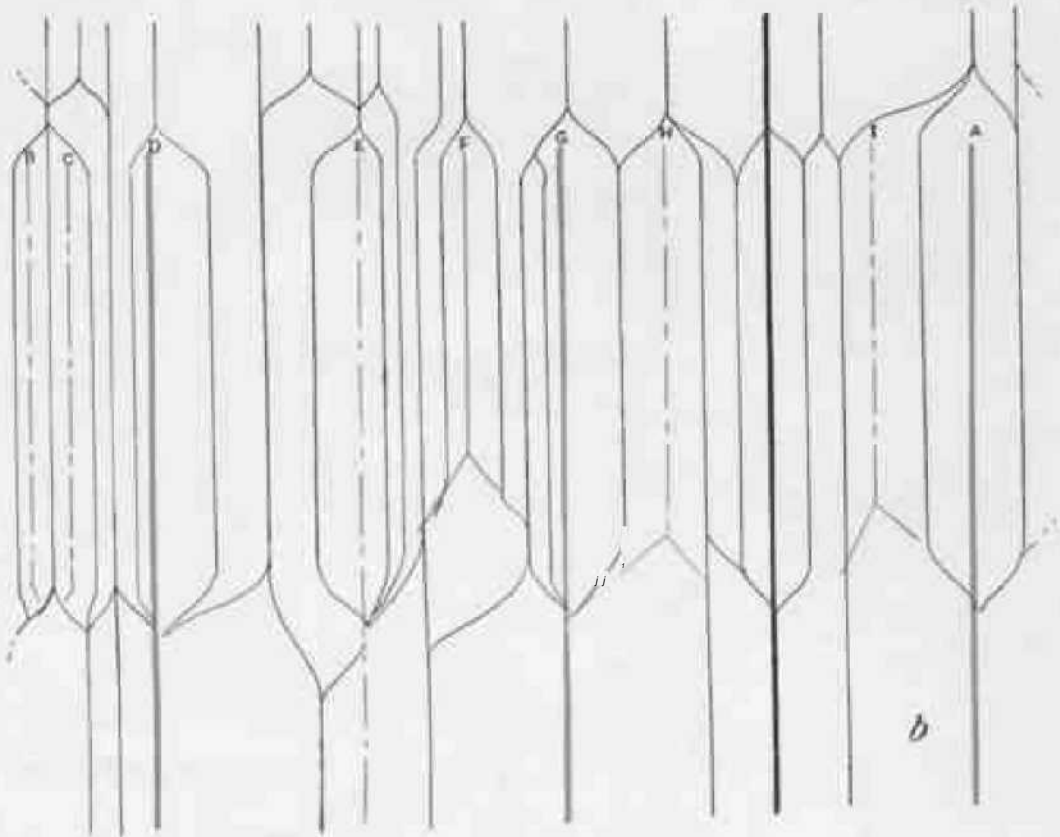
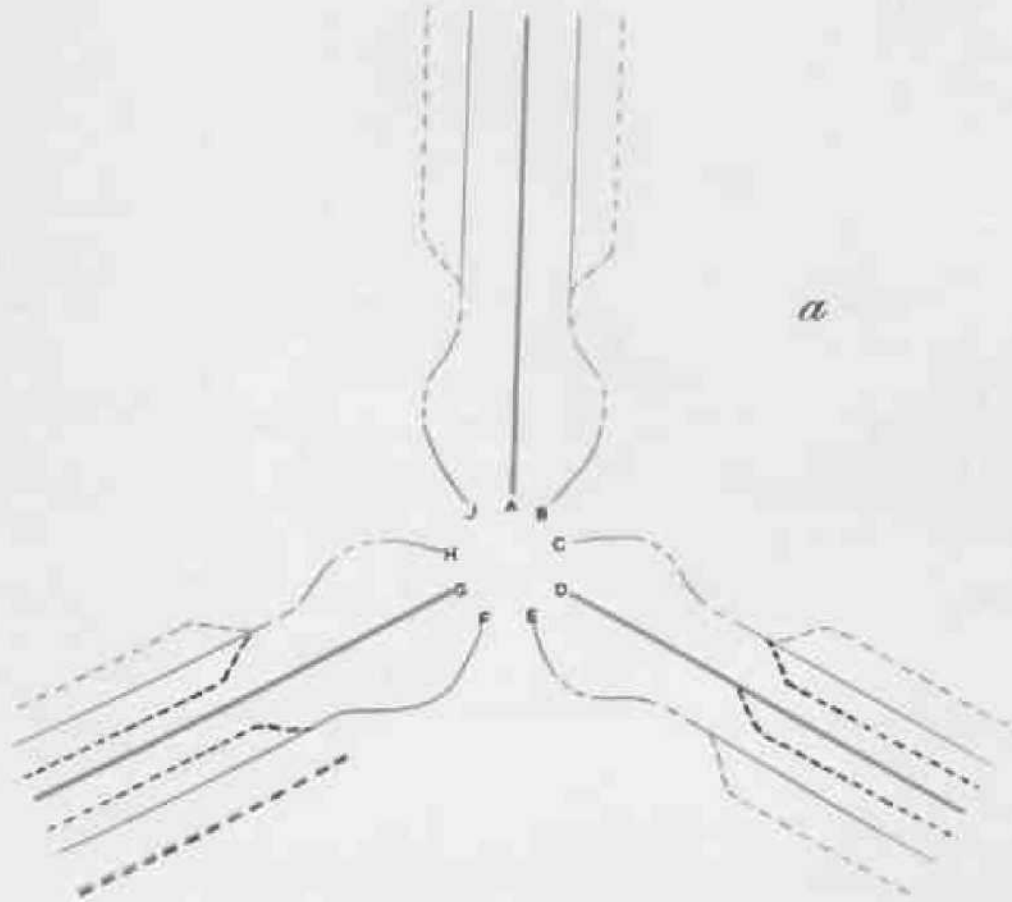




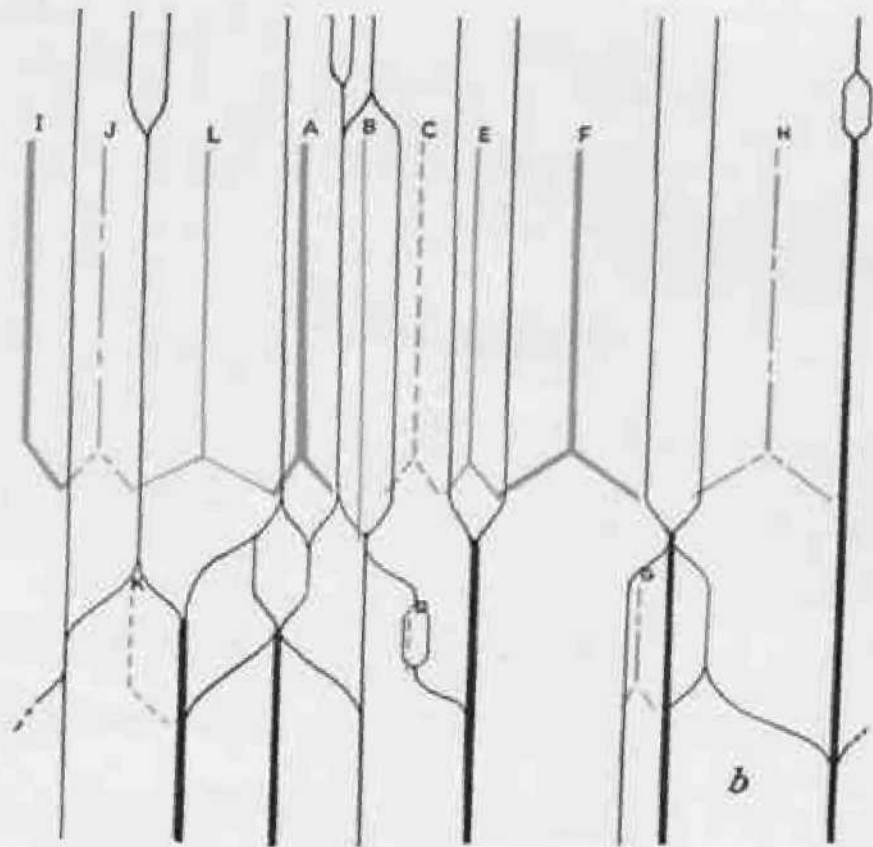
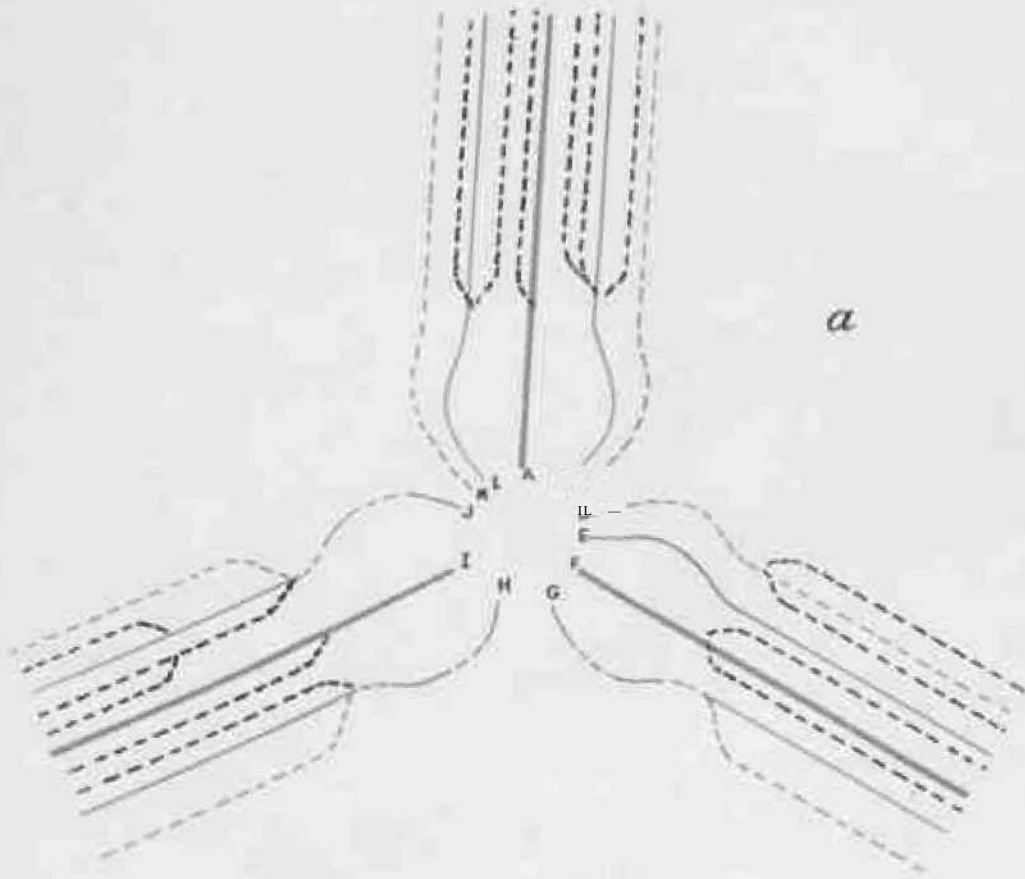
**ANEMONE PALMATA.**



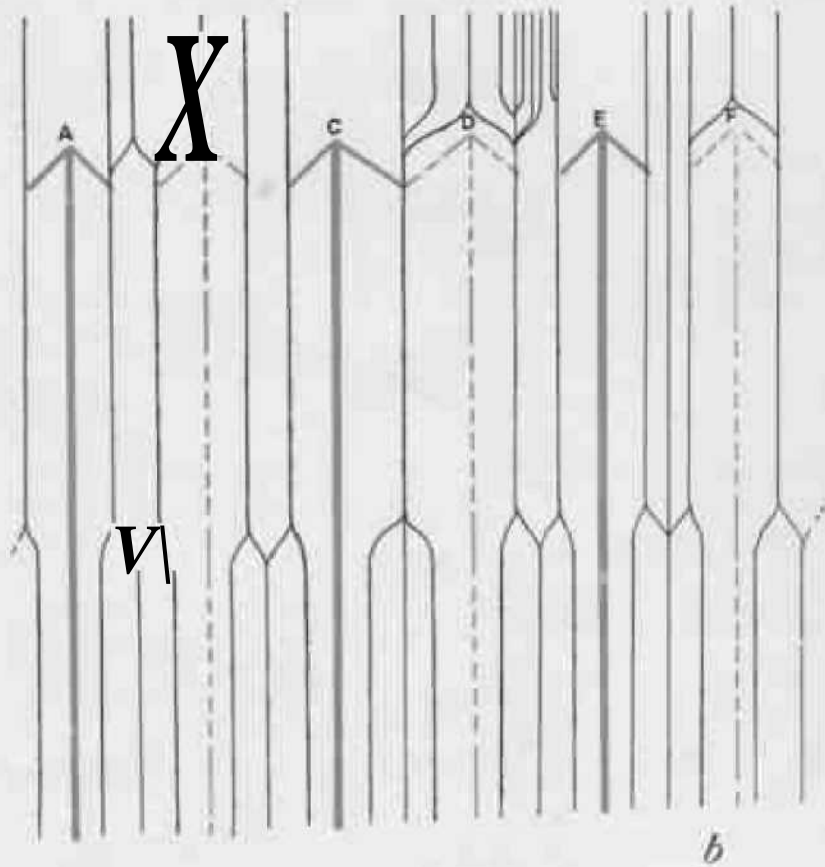
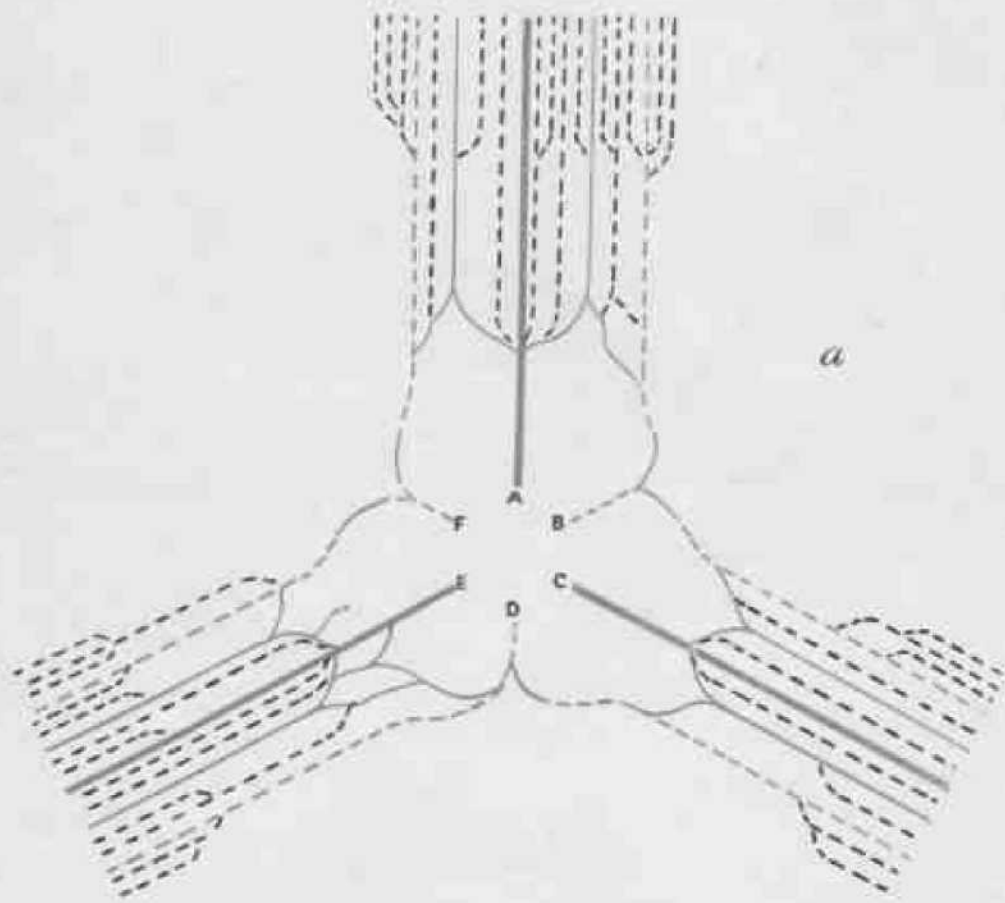
ANEMONE AITGULOSA.



ANEMONE HEPATICA,



RAKDNCUWJS FICAMA.



ERANTHIS HYEMALIS.

## The Pimpinellas of Tropical Africa. By CECIL NORMAN, F.L.S.

[Read 6th January, 1926.]

The following is an attempt to give a systematic account of the Pimpinellas of Tropical Africa. As in all Tropical African genera, the number of described species has largely increased in recent years. Five species were dealt with in the *Flora of Tropical Africa*, (1877)—thirty-one are considered here, I have had access to the material at the British Museum and Dewey, and, thanks to the kindness of Dr. A. B. Rendle, I have seen the types or authentic material from Berlin of species not in this country and unobtainable material from Brussels. To all concerned I here tender my thanks, in spite of all, more specimens are much needed, some species being known from only one plant, some from only one gathering. Still, it is hoped that this paper will prove useful, if it is only by bringing together in one easily accessible place the species so far known, and thus enabling the future worker to avoid—or, at any rate, to beware of—some of the pitfalls that beset his path.

*Pimpinella* is a widely-spread Old World genus, occurring in Europe, Asia with the out-tropics or on elevated regions within, and in Africa and the neighbouring islands. There are perhaps some 150 species, in Africa it occurs in the botanical regions, though very sparingly (as regards species) in North and South Africa—about four species in each. In the tropical region it occurs, or may do so, wherever the elevation ranges from about 3000 ft. to about 10,000 ft., provided there is sufficient rainfall. It is probably owing to its generally very low elevation that no species (so far as known) has been found in the vast tract of land west of the Cameroons (excluding N. Nigeria), and owing to its generally high elevation that the rest of the tropical region is so rich in this essentially temperate genus.

It appears that the species, for the most part, are restricted in range, but there are several notable exceptions: e. g., *Pimpinella oreophila* occurs on the Cameroons Mts., Mt. Melangi (in Nyassaland), and on the mountains of Abyssinia; *P. JBuchananii* in Nyassaland, Belgian Congo, and Angola, being probably the commonest Tropical African species. Only one species occurs in both Tropical and South Africa—viz., *P. castra*. This plant, originally collected in Natal, occurs also on the mountains of Abyssinia, but nowhere in between, so far as is yet known—a most interesting example of interrupted distribution. Has the migration been from north to south or from south to North? (South Africa easily represents the southern limit of the genus.

In no other part of the world does it reach as far south as the tropic of Capricorn.)

No species are common to North and Tropical Africa.

All the Tropical African species, except two, belong to Drude's subgenus *Eu-pimpinella*. This he divides into the two sections: i. *Tragoselinum*, with glabrous ovary; ii. *Tragium*, plants with hairy ovary. As regards the second section, it should be remembered that the presence of hairiness is determined in the early stages of growth, as in some species it disappears as the plant matures. The sections are subdivided into (a) species with simple, (b) species with pinnate root-leaves.

Here it should be noted that many simple-leaved species often exhibit one or more trifoliate leaves mixed with the simple ones—probably all do so at times. Apparently it may be taken that trifoliate root-leaves indicate simple-leaved species\*, even if no simple leaf is found on a particular specimen. The pinnate-leaved plants, on the contrary, though showing much variation in the root-leaves, seem always to maintain the truly pinnate character. These remarks apply, of course, only to the plants under consideration.

### *Descriptive Key of the Species.*

Subgenus EU-PIMPINELLA Drude, in Pflanzenf. iii. pp. 8-196. Petals obcordate, with folded apex white or reddish, rarely yellow; style as long as or usually much longer than the stylopodium, which is conical and free from the calyx. Bracts and bracteoles usually wanting. Fruit smooth and glabrous, or hairy.

I. Section *Tragoselinum* DC, Prod. iv. p. 199. Ovary glabrous.

A. Radical leaves normally simple (see remarks above).

i. Radical leaves suborbicular or subtriangular.

- » » ±5-6 cm. long and across the base; stem quite glabrous. . . . . 1. *V. fltM*\*\*
- » *II* +3-6 cm. long and 8-4 cm. across the base; stem densely pubescent. . . . . 3. *P. cqfra*.
- » » w +2 cm. long and 1\*5 across the base; whole plant quite glabrous. . . . . 2. *P. negUcta*.
- » » ±1 cm. long and across base; plant pubescent. . . . . *T^HM*, *^PMUmandschartca*
- ii. Radical leaves oblong-lanceolate. . . . . 6. *P. trifnrkata*
- iii. Radical leaves usually siniform; teeth long, apiculate. . . . . 7. *P. acutidentata*;
- iv. All lower leaves trifoliate. . . . . 5. *P. Jcyimbilaensts*.

B. Radical leaves pinnate.

i. Pedicels thick and stout (at any rate in fruit).

- Leaflets orbicular (margins crenate). . . . . 11. *P. oreophifa*
- „ lanceolate or ovate-lanceolate; umbel rays up to 3 cm. . . . . 8. *P. Stolzii*

\* *P. etbaica* seems a possible exception.

- «• Pedicels always hair-like.
    - Leaflets ovate-lanceolate, petiolate; umbel rays not above
      - 1\*6 cm. . . . . 9. *P. Buchananii*.
      - » broadly linear, subcordate, sessile. . . . . 10. *Rfavifolia*.
      - tt ±orbicular (margins acutely dentate). . . . . 12. *P. keniensis*.
  - C. Radical leaves pinnatisect. . . . . 13. *P. HombUi*.
  - II. Action *Tragium* DC, / . c. Ovary hairy.
    - A. Radical leaves normally simple (see remarks above).
      - \* Perennials or Biennials.
        - 1. Umbel rays very many, exceeding 12 (except in *P. Ledermannii*), thick and upright; flowers very numerous, more than 20, with many males in each partial umbel.
          - «• Umbel rays glabrous, more than 12.
            - Radical leaves thick and fleshy.....14. *P. Gossweileti*.
            - a „ thin; petioles glabrous or nearly so.
            - » „ up to 14 cm. broad; base widely cordate. . . . . 15. *P. Mechowii*.
            - it <sub>f</sub> ±5 cm. broad; base truncate. . . . . 16. *P. robusta*.
            - Petioles densely pubescent.
            - Radical leaves: base cordate, with narrow sinus .... 17. *P. platyphylla*.
          - \* Umbel rays hairy.
            - Rays ±20. . . . . 18. *P. Engleriana*.
            - Rays 7 or fewer. . . . . 19. *P. Ledermanii*.
        - 2. Umbel rays few, less than 10 (except in *P. Volkensii*) flowers ±12 in each partial umbel, hermaphrodite.
          - «• Stem and rays glabrous.
            - 1. Fruit with closely-appressed hairs.
              - Leaves and petiole quite glabrous. . . . . 22. *P. Volkensii*.
              - „ <sub>y</sub> pubescent, especially the petioles. . . . . 20. *P. huilensis*.
            - »• Fruit with spreading hairs. . . . . 21. *P. Welwitschii*.
          - 5. Whole plant cinereo-pilose. . . . . 23. *R* <sup>Λ</sup> *iva*.
        - \*\* Annual, very slender, ±15 cm. high. . . . . 24. *P. tenuissima*.
      - B. Radical leaves pinnate.
        - P<sub>lant ne</sub> arly glabrous, hairs on fruit appressed; leaflets closely toothed, thin. . . . . 26. *P. P<sup>Λ</sup>aventa*.
        - »> scabrid, hairs on fruit straight!. . . . . 26. *P. P<sup>Λ</sup>egrina*.
        - w softly pilose, hairs on fruit hooked. . . . . 27. *F. camptotneha*.
        - » nearly glabrous, hairs on fruit hooked, leaves pinnatisect. 28. *P. etbaica*.
        - " pubescent, ovary sparsely hairy, leaflets ± deeply incised. 29. *P. nandensis*.
- Subgenus RKUTEBA (Boiss) B. & EL, as subgenus in Gen. PI. i. p. 894. Leaves pinnate, segments toothed or dissected; flowers yellow (or white in Trop. Afr. species). Fruits glabrous or papillose, bracts and bracteoles conspicuous in Trop. Afr. species.
- Fruit minutely papillose. . . . . 3a *R* <sup>\$</sup> *imm* <sup>TM</sup>
  - , glabrous, smooth. . . . . 31. *P. imbnkata*.
- LI<sub>K</sub>\*. JOURN.—BOTANY, VOL. XLVII. 2 Y



PIMPINELLA Linn. Syst. ed. 1 (1735).

Benth. & Hook, f., Gen. Plant, i. p. 893.

Engler & Prantl, Pflanzenfam. iii. pp. 8-195.

Subgenus EU-PIMPINELLA Drude.

Section I.—Tragoselinum. Fruit glabrous.

1. *P. FILIFORMIS* Wolff, in Fedd  Rep. xvi. p. 237 (1919).

*P. pseudo-caffra* Norm, in Journ. Bot. lxi. p. 134 (1923).

Belgian Congo: in damp places, Kundelungu, *Kassner* 2783.

A distinct species, characterized by the tall slender terete stem and large leaves.

2. *P. NEGLECTA* Norman, sp. nov.

Planta humilis perennis, semi-procumbens, omnino glabra ; radice elong<sup>ta</sup> fusiforme sub-lignosa, caule ramoso, foliis radicalibus simplicibus, brevity petiolatis, oblongo-orbicularibus basi leviter cordatis, margine acute dentatis; foliis caulinis ad bracteas vaginantes reductis ; umbellis magnis  $\pm 6$  radiatis, radiis longis crassis aequalibus ; umbellulis  $\pm 9$  pedicellutis, pedicellis crassiusculis ; involucro et involucello nullis ; petalis flavis (ex coll.) »P<sup>lce</sup> inflexis; ovario glabro, stylopodio piano stylis brevissimis.

*Principal measurements.* Leaves  $\pm 2$  cm. X 1-5 cm.; petioles about 2 cm-long ; radii 2-3 cm. long.

*Hab.* Rhodesia: Mazoe District, alt. 4200 ft., September 1906, *Eyb*<sup>\* ioi</sup> in Herb. Mus. Brit, (type) ; « between Broken Hill zinc mine and Swan Micuba copper mine," C. E. F. Allen in Herb. Kew, sine no. ,..

A well-marked species, readily distinguished by the lax habit, long rad<sup>\*</sup>  " yellow flowers/" acutely toothed leaf-margins, and in being compleW glabrous. Apparently allied to the next following.

3. *P. CAFFRA* D. Dictr. Syn. Pl. ii. M. 947.

*Hab.* S. Abyssinia: between Haarar and Addis Ababba, *Capt. M-* °\* *Wellby, t. n.* in Herb. Kew ; also in Natal.

The whole plant is densely pubescent except the fruit, which sometime<sup>9</sup> has a few scattered hairs.

*Capt. Wellby's* plant is indistinguishable from plants from Natal a<sup>'\*1</sup> extreme east of Cape Colony. It appears to be the only known specimen from Abyssinia, but there is no evidence of any mistake, so the facts may " , accepted, at least provisionally, as a most interesting case of interrupted distribution. At the same time confirmation is urgently desired.

4. *P. KILIMANDSCHARIOA* Engler, in Bot. Jahrb. xix. Beibl. n. 47 (<sup>1894</sup>) p. 42.

*Hab.* Kilimanjaro : « 3200-3400 metres in the Johannes Gorge and open grass-land above," *Volkens* 1196.

An erect plant of low stature with obtusely orenate leaf-margins and rather dense pubescence, especially on the radii and petioles.

<sup>5</sup>« P. KYIMBILAENSIS Wolff, in Fedd  Rep. xxii. p. 348 (1926).

*Sab.* Kyimbila District, Tanganyika Territory, *Stolz* 2512 in Herb. Mus. Brit. and Kew.

There are no radical leaves preserved, but they are probably simple. Apparently allied to and certainly a good deal like *P. ebracteata* from Madagascar.

<sup>6</sup>\* P. TRIFURCATA Wolff, *I C.*

*Sab.* Kyimbila District, Tanganyika Territory, *Stolz* K. 14 in Herb. Mus. Brit. and Kew.

The root-leaves somewhat recall the stem-leaves of *P. Ledermannii* in shape «'» tothing, though the two are widely separated. There is much variation in shape and tothing of the leaflets of the stem-leaves.

<sup>7</sup>• P. ACUTIDENTATA Norman, sp. nov.

Herba tenuissima perennis circa 35 cm. alta, caule terete interne sparsissime Pubescente, superne glabro; *foliis basalibus* nervis subtus pubescentibus, ««e glabris, reniformibus," vel rarius subtriangularibus basi leviter ewavatis, marginibus dentatis, dentibus longe apiculatis, interne valde "ticuktis, petiolo brevionnino vaginante suffultis; *foliis caulinu* paucissimis <sup>a</sup>«i bracteas vaginantes reductis, vel nullis; *umbellis* exinvolucratis magnis, ±5 radiatis, radiis inaequalibus patentibus ; *umbellulis* exinvolucellatis ±7 Pedicellatis, pedicellis filiformibus, subsequialibus: petalis minutis, *stylis* ^ngiuscnlis, *stylopodU* parvo sub-piano; *fructufto* genere magno, rotundato glabro.

*Principal measurements.* Reniform leaves to 5 x 6\* cm. ; triangular leaves <sup>n</sup>P to 6 x 5-5 cm. (across the base) ; petiole 2-3 cm.; radii 3-6 cm.; pedicels ±4 mm.

*Hab.* Belgian Congo : "Region da La^laba, Katanga," *HombUim* (type) \*» Herb. Brux. ; Upper Katanga, *A. Hock*, s. n.; Valle de la pet.te Luemba, <sup>A</sup>- *Hock*, s. n.

Somewhat like *P. plat^Ua*, but separated by the fruit. The leaves ar. "emarkable for the long slender teeth. Of the five specimens seen, all have r«oiform leaves except one of the two plants on the type-sheet.

<sup>8</sup>- P- STOLZII Wolff, in Engler's Jahrb. Ivii. p. 277 (1922).

o «A Nyassaland : N. end of Lake Nyassa near Langenburg, 1000. m., \*\* 692/ Belgian Congo: Elizabethville, *Beguaert* 297 :n Herb. Br»x

us Unfortunately I have seen no authentic material the scrap:nt Kew beu\* large\*» but from the description I place Bequaert's -I-''TM'' ^ TM true r leaves, and especially the much longer umbel rays, J ^ upg of the disU ncti;ns from p. BmUnann. I do not noface much pedicels, referred to by Wolff.

9. *P. BUCHANANII* Wolff, in Engler's Jahrb. xlviii. p. 269 (1912), and Jahrb. lvii. p. 227 (1922).

Nyassaland, *Buchanan* 709 ; Mulinda Plateau, 900 m., *Stolz* 1449\* ; JShire Highlands, Zambesia, *Buchanan* 268. A vigorous specimen leaflets up to 7 cm. long.

Belgian Congo, *Kassner* 2478. This specimen is more hairy on the lower stem and petioles than any of the others ; but this is easily accounted for its being a much younger plant—it is not yet fully in flower, the leaflets exactly match *Stolz* 1449 in shape and tothing, but are somewhat larger.

Elizabethville, *HombU* 203 in Herb. Brux.

10. *P. FAVIFOLIA* Norman, in Journ. Bot. lxi. p. 133 (1923).

Belgian Congo : Kasenza River, Lake Mweru, *Kassner* 2818.

This, though perhaps allied to *P. Buchanania*, of which it has the pedicels and the fruit, is quite unlike any other *Pimpinella* I have seen. leaves are very remarkable ; unfortunately, they are badly pressed and difficult to describe. The leaflets are sessile, close together and subbroadly linear or linear-lanceolate ; apiculus and teeth horny, The plant about 4 ft. high and certainly not an annual as originally suggested.

11. *P. OREOPHILA* Hook f., in Journ. Linn. Soc. vii. p. 195 ; Hiern, m Trop.Afr.iii. p. 14 (1877).

*Hob.* Fernando Po, 9500 ft., *Mann* ; Cameroon Mountains, 10,000 ft., *Mann* ; Abyssinia, 10,000 ft., *Schimper* 1502.

A rigid plant with crenate margins to the leaflets.

There is a plant at Kew, *Adamson* 370, from Mount Melange (6774) with narrow incised leaflets which I take to be a form of *P. oreophila* not so upper stem leaves often show an approach to this form, if they are times identical with it.

The distribution is very remarkable.

12. *P. KENIENSIS* Norman, sp. nov.

Herba perennis circa 23 cm. alta radice fusiforme, caule ram(??) sparse pubescente, foliis basalibus pinnatis 2-3-jugatis petiolo piloso ; toliis orbicularibus subtus praesertim sparse pubescentibus, sessilibus vel subsessilibus, marginibus dentatis, dentibus acutis apiculatis, basi truncatis vel affoliolo terminali lateralibus vix superante ; foliis caulinis ad bracteas vaginatas pinnatas reductis ; umbellis ± 6-8 radiatis, radiis tenuissimis, pedicellis tenuibus 6-9, involucro et involucellis nullis ; petalis aoi, glabro, stylopodio piano, stylis brevibus.

*Principal measurements.* Leaf with petiole 4-6 cm. ; leaflets ± J-long and broad ; umbel rays 1-1 • 5 cm.

\* Sent out from Berlin as *P. Engleviana*, but referred to *P. Buchanania* by Wolff in Engler's Jahrb, lvii. p. 228, no doubt rightly.

**Hab. Kenya** Colon<sup>3r</sup> Mrs. Prescott-Decie (type); Hills about Kikuyu, Scott-Elliott 6739 Herb. Kew.

All<sup>1</sup> mar<sup>le</sup> d<sup>10</sup> P<sup>1</sup> oreo<sup>phila</sup>, but readily distinguished by the acutely-toothed gins of the leaves and the slender rays.

13<sup>1</sup> P<sup>1</sup> H<sup>o</sup> MBLEÍ Norman, sp. nov.

erba<sup>1</sup> P<sup>erenms</sup> á<sup>á</sup> > o<sup>i</sup> ca 4 ped. alta, omnino glabra radice lignosa, caule sectis Q<sup>nt</sup>erne SU<sup>á</sup> cato, <sup>ev</sup> <sup>er</sup> ramoso, foliis basalibus profundissime pinnatisem<sup>is</sup> U<sup>a</sup> atls se<sup>g</sup> mentis longissimis, linearibus acutis ad "8-1 \*4 cm. inter Mils<sup>is</sup> <sup>nar</sup> <sup>g</sup> <sup>h</sup> <sup>k</sup> <sup>us</sup> remote acuteque serratis petiolo breviter vaginante, radiis <sup>ms</sup> <sup>s</sup> <sup>m</sup> <sup>á</sup> <sup>k</sup> <sup>us</sup> sed minoribus, umbellis exinvolucratis ±6 radiatif P<sup>dic</sup> <sup>ill</sup> <sup>s</sup> <sup>filif</sup> <sup>o</sup> <sup>r</sup> <sup>m</sup> <sup>á</sup> <sup>us</sup> P«tentibus, umbellulis exinvolucellatis ±10 pedicellatis flavis ( <sup>o</sup> <sup>ll.</sup> ), s<sup>á</sup> o<sup>podio</sup> sub-piano, stylis brevibus fructu (immaturo)

<sup>inc</sup> <sup>measurements</sup> - Leaves, including petiole, pup <sup>p</sup> 22 cm. long; leaf-<sup>g</sup> <sup>ment</sup> <sup>s</sup> <sup>UP</sup> <sup>to</sup> 16<sup>c</sup> m. long and ±3-"6 cm. broad (the terminal segment J<sup>offer</sup> <sup>tn</sup> <sup>UP</sup> <sup>to</sup> 16<sup>c</sup> m. long and ±3-"6 cm. broad (the terminal segment

Sab. <sup>T</sup> <sup>g</sup> <sup>ia</sup> ? C<sup>o</sup> <sup>n</sup> <sup>g</sup> <sup>o</sup> : " YaJU\* de KaPiri>" Katanga, fliwwWrf 1225.

This spec<sup>IGS</sup> <sup>AS</sup> <sup>rema</sup> rkable for the pinnatisect leaves, which in appearance somewhat rCCa11 <sup>á</sup> <sup>SP</sup> - The first is quite immature, but the plant has all the charact. <sup>á</sup> <sup>f</sup> <sup>u</sup> <sup>p</sup> 4 inella.

Section II.—Tra<sup>glum</sup> > Oyar<sup>á</sup> haif<sup>á</sup>.

14 <sup>P</sup> <sup>á</sup> <sup>GOSSWEILERI</sup> Wolfe, in Fedde Rep. xvi. p. 234 (1919).

Goss<sup>Ni</sup> <sup>Ban</sup> <sup>g</sup> <sup>o</sup> Malange, "in high grass skirting the Pandanus/"

tho<sup>is</sup> <sup>á</sup> <sup>pecies</sup> is remarkable for its thick flosly louvos, peculiar serration, and Agreeable smell of the whole pl<sup>á</sup>It (Gossweiler).

15 <sup>f</sup> <sup>á</sup> MECHOWII (Engl.) Wolff, in Engler's Jahrb. lvii. p. 226 (1922).

• <sup>á</sup> <sup>elwitschii</sup> Engl., var. *Mechowii* Engl. Hochgebirges Fl. p. 319 (1892).

<sup>A</sup> <sup>T</sup> <sup>á</sup> <sup>go</sup> ]<sup>a</sup>: Melange, *Meclww* 471 in Herb. Berol.

t<sup>extu</sup> <sup>G</sup> <sup>root</sup> <sup>l</sup> <sup>á</sup> <sup>aves</sup> are larger than in any other African species and thin in

\*Uh<sup>re</sup> <sup>P</sup> " <sup>á</sup> <sup>olff</sup> <sup>has</sup> <sup>n</sup> <sup>g</sup> <sup>htly</sup> <sup>raised</sup> <sup>i</sup> <sup>\*</sup> <sup>to</sup> the rank of a species; the affinity js

• *Vossweileri* and its allies, and not with *P. Welwitschi*L

16. <sup>P</sup> <sup>KOBUSTA</sup> Norman, in Journ. Bot. ix. p. 119 (1922).

<sup>An</sup> <sup>gola</sup>: Cuanza norte District, between Angage and Camabatela, Gossweiler 7473.

Remarkable for the round stiff stem, and especial<sup>á</sup> for the V6ry lar

\*H <sup>á</sup> <sup>elope</sup> <sup>d</sup> <sup>10</sup> <sup>W</sup> <sup>8</sup> <sup>r</sup> <sup>stem</sup>, leaves <sup>á</sup> <sup>trifoliate</sup> with coarse sharp tothing, and not he largest species. The affinity is with the two preceding species, <sup>á</sup> <sup>h</sup> <sup>P</sup> <sup>Welwi</sup> <sup>Uchii</sup> as stated in the original description.

17. *P. PLATYPHYLLA* Welw. ex Hiern, Cat. Welw. Afr. PL i. P. 426 (1900).

*P. Welwitschii* BngL, var. *Buchneri* Engl., in Hochgebirges J:1. P. 19. 81  
 Angola: Pundo Andongo, *Welwitsch* 2504 ; Melange, B n \* 1 ^  
 Herb. BeroL

The stem-leaves are rather large, either almost orbicular or oblong-orbicular; the sinus at the base narrow and rather deep.

18. *P. ENGLERIANA* Wolff, nom. nov. in Herb. BeroL

*P. tomentosa* Engler (non Walz.), in Jahrb. xxx. p. 368 (1901)-  
*Hab.* Tanganyika Territory : Usagara, *Goetze* 1125 in Herb. BeroL.  
 The densely cinereo-pilose umbel rays are the distinguishing feature.

19. *P. LEDERMANNII* Wolff, in Engler's Jahrb. xlviii. p. 270 (1912).

*P. Tessmannii* Wolff, in Fedd & Rep. xvii. p. 170 (1921).

*Hab.* Cameroons : Markt Singwa, *Ledermann* 1620 (without root-leaves);  
 Ngaundere, *Tessmann* 2711 (with root-leaves). Both in Herb. BeroL.

Easily recognized by the short and few umbel rays (in all the allied species they are very many) and the narrow oblong lower stem-leaves.

Having seen the type-specimens of both *P. Ledermannii* and *Jr. Tessmannii* it seems to me that they are one and the same species, *Tessmann* supplying the root-leaves that were missing in *Ledermann*'s. The umbel rays in *P. Tessmannii* are rather more slender than in the other, but *Tessmann*'s plant is in a younger state, which would account for this. The root-leaves of *P. Ledermannii* as here understood are much like those of *P. platyphylla*.

20. *P. HULLENSIS* Welw. ex Engler, in Hochgebirge's J:1. P. 19. (1892)

*Hab.* Angola : Huilla, *Welwitsch* 2502.

This plant is remarkable for the very closely appressed hairs of the fruit. It was this character, I suppose, that caused *Welwitsch* to describe the fruit as "muriculate." Certainly the appearance of the fruit is unusual; the hairs are very deciduous, so that the ripe fruit is glabrous (except on the ribs), and the styles are remarkably short.

21. *P. WELWITSCHII* Engler, *l. c.*

*P. huillensis* Engl., var. *elatior* Welw. ex Hiern, Oat. Welw. p. 426.

Angola: Huilla, *Welwitsch* 2503, 2503 b ; *Gossweiler* 3128 (no locality), 3177 (near Kutchi) ; *Wellman*, Bailundo District, Herb. Kew.

The hairs on the fruit of this species are thick and spreading, and somewhat deciduous, much less so than in the last, and the styles are rather long. On these characters only it is here separated from *P. huillensis*.

22. *P. VOLKENSH* Engler, in Pflanschw. Ost. Afr. 0 299 (1895).  
 Kilimanjaro, 3200 m., *Volluns* 2025 ; < 3rd day from Eldona Rav. n<sup>e</sup>,  
 \* ¥ • in He p. Kew; Mt. Kenya, 6500 ft., *Battucombe* 725 m Her<sup>b</sup>.  
 K«w: a stouter plant showing many trifoliate leaves, presumably  
 species.  
 Usually a smaller and much more slender plant than any of its near aiue .

23. *P. RIVA* Engler, in Ann. 1st. Bot. Rom. vii. p. 22 (1898).  
 Somaliland: between Alge and Oi, *Riva* 1237 (in Rome ?).  
 No specimen seen.

<sup>2</sup>\*. *P. TENUISSIMA* Norman, sp. nov.

*Herba annua* (ut videtur) *humilis* circa 15 cm - ^ << ^ \* £ t a i Z C  
 Pubescente demum glabro, ran.oso; foliis rad.cahbu<sup>s</sup> simphebo<sup>s</sup> - liis  
 tt-gBhrfta. basi profunde cordatis, marginibus letter dentos<sup>is</sup>, \* ..  
 -nlinis multinodis l<sup>i</sup>foliolatis, foliolis sessilibus vel - £ — S ^  
 g'nibus dentatis (vel rarius integns) laterahbus SUP<sup>rhomb.</sup>  
 Weolatis, terminalibus late vel anguste lanceolate et lateralibus semper  
 "cedentibus; umbellis 4-6 radiatis, radiis glabris "alde in ualibus,  
 "nbellulis 8-10 pedicellatis, pedicellis in^qualibus , ^ " ^ . I W  
 n ^ ; petalisalbisapice inflexis, ovario pilis longis albidis oblecto, sty  
 Podiff. cericis conspicuis ; stylis longis patentibus.

*Principal meaZements*. Base-leaves 2 cm. x 1-5 (across the base) ; e tiote  
 ±3 cm.; stem-leaves: terminal leaflets ±1X "7 on., lateral ± 8 x 5

om.  
*Eri* -: Mont Bosco, pres Saati, *Sehwein/urh* & *Riva* 569 in Herb. Kew.  
 A. pretty little plant, apparently related to *P. eriocarpa* from Syria and  
 Mesopotamia.

<sup>1</sup>\*. *P. PRÆVEKTA* Norman, sp. nov.

*Herba* gracilis 1-3 ped. alta (ex coll.), - \* ? T J ^ nisx<sup>mis</sup> madmis,  
 f - » « pinnatis, ambitu triangularibus 2-vel ^ - ^ t K S sessilibus  
 lo » gmscule petiolatis, petiolulis rachideque pubescentibus. ce truncatis  
 '6 I ^ sessilibus ; laminis membranaceis, lanceolate " » TM » | ^ , rae  
 'J' Witer attenuatis, marginibus arete • j J ^ | T ^ , ' J i T l i  
 £ > \* » , bfeme pilis rigidulis (nervis prsertim) sparse ... tenu iggimis  
 P<sup>is</sup> imi8 s ^ n . ^ a , exin volucratis ± ^ d w ^ ' X 3 l . tii nmlti-  
 P<sup>atibus</sup> sub^qualibus demum glabris; umbelluhs exinvo<sup>o</sup> : hermaph rodui  
 ^ cellatis pedicellis pubescentibus valde n.«q»hb«<sup>o</sup> . ^ i " B  
 alb ^ ¥ Mongissimis reflexis, ovario pilis valde f ^ p ole); lowest  
 J W W W B ^ . Radial leaves up to 13 cm. (TM<sup>l</sup>TM<sup>m</sup>J> P<sup>tiote,lowest</sup>  
 ff\* . 3 cm. x 1-1.5 cm.; topmost leaflets 2 cm. x 1 m ^ P«  
 leafle<sup>te</sup> '7 cm.; umbel rays up to 2 cm.; pedicels up to 5 cm.

*Hab.* N. Nigeria: Vom, Bauchi Plateau, alt. 3000-4500 ft., *J. Dent Young* 107 in Herb. Kew.

A very distinct species, the thin delicate leaves being unlike any other in texture and tothing; moreover, it is so far the only Nigerian species.

26. *P. PERBGRINA* Linn. Mant. ii. p. 357.

*P. hirtella* A. Rich. Flor. Abyss., i. p. 323 (1847).

Abyssinia, *Schimper* 272, 6200 ft.; 355. Also in South Europe and Asia Minor.

The African specimens do not seem to differ in any way from those of Europe and Asia.

27. *P. OAMPTOTRICHA* Penzig, iii Atti Oongr. bot. Genova, (1893), *P. Erhruit*, " *Capt. H. Lynes*, R.N. (*sine no.*).

No authentic material has been seen, but the plants seem to agree with the original description. The lower parts are softly pilose, with an obvious distinction from *P. peregrina*: in Admiral Lynes's plant the rays are noticeably shorter than the plant from Saganeiti.

28. *P. BTBAICA* Schweinf., in Verh. Zool. Bot. Wien, ser. i. p. 667.

Nubia: Soturba hills, *Schweinfurth* 7474; Red Sea Province: Kamobran *MacDougal* *fy Sykes* 86.

The leaves of this species are most variable, sometimes pinnately triplicate, sometimes trifoliate, with deeply-incised segments; sometimes the segments are linear.

29. *P. NADENSIS* Norman, sp. nov.

Herba perennis? pubescens vix ramosa, caule striato; folds basalibus caulinis (nisi supremis) consimilibus, pinnatis  $\pm 5$  jugatis, foliis sub-orbicularibus vel sub-triangularibus sessilibus, superioribus approximatis ad 1.5 cm. remotis, margine profunde vel leviter incisim utrinque pubescentibus, petiolo basi late vaginante (vagina ad 2 cm. Umbellis exinvolucratis, magnis  $\pm 6$  radiatis, radiis crassis densius pubescentibus; umbellulis exinvolucellatis multipedicellatis, pedicellis usculis, petalis albis, stylopodio subplano, stylis longiusculis, ovario pubescente. *Fructus maturus ignotus.*

*Principal measurements.* Leaves with petiole up to 8 cm.  $\pm 1.5 \times 1$  cm.; rays up to 3 cm.

*Hab.* Nandi, 7000-8000 ft., *Scott-Elliott* 6975 Herb. Mus. Brit. Kilimanjaro, 3000-4000 ft., *Janssens* Herb. Brux.

This species can be readily distinguished from *P. keniensis*, which it more or less resembles by its thick and pubescent umbel rays as well as by the cutting of the leaflets, which is always variable. I suspect that the up-fruit may prove glabrous, at least sometimes, as the ovary is only sparsely





Studies in the Phytoplankton of the Lowland Waters of Great Britain.

No. V. The Phytoplankton of some Norfolk Broads. By BENJAMIN MILLARD GRIFFITHS, D.S.C., F.L.S.

(11 Text-figures.)

[Read 12th May, 1926.]

INTRODUCTION.

BETWEEN Norwich and the sea there lies a large triangular area of low-lying land which in Roman times was a broad and shallow estuary. The estuary was originally formed in the period when the area now occupied by the North Sea was slowly submerged below tide-level. In Roman times, when the tide was out, the estuary presented the scene of wide mud-flats, through which wandered the rivers Bure, Yare, and Waveney. When the tide came in the estuary became an expanse of water with a few very low islands rising from beneath the surface. The tidal drift off the coast ran southwards the coastal detritus and the sediments brought down by the rivers were carried by the tidal drift, and formed a bar across the mouth of the estuary. In the course of the centuries the bar grew larger until it formed an almost complete barrier, and the river-silts tended more and more to be dropped on the floor of the estuary behind the barrier. The final result was a change of the estuary into an area of very low marshy land, diversified with a few islands of slightly higher ground, and penetrated by slow-flowing rivers (see Marr, 16, p. 165). The barrier formed the site upon which Yarmouth now stands. The old levels were not greatly affected by the changes, and the fall from Norwich to the sea is still only about two inches (Pallis, W, p. 218). The tide-water does not now come into the estuary because the great barrier at the mouth leaves only a very narrow channel at the mouth, and the sea-water flows in at flood-tide so slowly that the ebb occurs before the sea-water has come far inland. It is only when there is an exceptionally high tide and an on-shore wind that the tide can be held up long enough to ensure penetration. On these occasions the heavy salt water creeps up under the lighter fresh water and causes a kind of under-flooding which may do great damage to freshwater fish.

The silting of the area and its conversion into fen was not complete. In many places there were slightly deeper hollows in the original mud-flats, where the depth of water was too great to allow the invading marsh vegetation to obtain a footing. These areas therefore remained as open stretches of fresh water, while the shallower areas became gradually filled up with vegetation, and their levels were slowly raised by the accumulation of vegetable detritus *in situ*. The areas of open water constitute the Broads.

There are some sixty of them, varying in depth from fifteen to thirty <sup>te\*</sup> and in area from one to twelve hundred acres. Many, but not all, are <sup>tidal</sup> waters in the sense that the tidal ebb and flow is perceptible, but not in <sup>the</sup> sense of being actually invaded by the sea-water. The tide comes m<sup>^</sup> Yarmouth and changes the outfall level, and the river-water accumulates, a time and the levels of the river and Broads are also raised <sup>P<sup>0</sup> 1 ? ^</sup>. The rise and fall amounts to two feet or more at Brundall, just be <sup>22</sup> Norwich. (For general account of the Broads, see Pallia, 17, PP- <sup>27</sup> 27.) The result of this geographical evolution is that the various Broads <sup>have</sup> different ecological histories and are differing habitats at the present <sup>da-</sup>. In August 1924 the writer examined the phytoplankton of the folio\* <sup>in</sup> B places in the area :—

Group A. Wroxham Area: River Bure at Wroxham Bridge ; Wro<sup>xham</sup> Broad; River Bure below Wroxham Broad; a small broad <sup>imme-</sup> diately above Salhouse Broad, referred to in the text as "Upper <sup>Upper</sup> Salhouse Broad."

Group B. Norwich Area: Surlingham Broad ; River Yare at Branda <sup>if</sup>, Rockland Broad.

Group C. Yarmouth Area: Ormesby Broad.

The collection was made by towing behind a rowing-boat a conical ne<sup>t</sup> <sup>^</sup> 0.05 mm. mesh bolting silk. The collections were preserved on the spot wi<sup>2</sup> 2 per cent, formalin. The choice of Broads was determined by considerate<sup>ns</sup> of accessibility. Many of the Broads can be reached conveniently only <sup>^</sup> sailing-boat or motor-boat. The results of this brief sampling of the ar<sup>of</sup> show that a more extended survey would undoubtedly yield a rich harvest <sup>of</sup> algae, particularly of Protococcales.

#### TOPOGRAPHY AND PHYTOPLANKTON t<

##### GROUP A.—The Wroxham Area.

###### River Bure at Wroxham Bridge.

The collection was taken just above the bridge at Wroxham. A\* \* <sup>h</sup> point the banks are bounded by wharves. Just above the point of collect<sup>n</sup> there is a small and weedy broad between the main road and the <sup>r a l l ^</sup> plankton contained much muddy detritus stirred up from the botto<sup>^</sup> by river traffic, and also some amount of vegetable detritus. There w<sup>^</sup> numerous dead and empty specimens of *Surirella*, *Gyrosigma*, *Campyl*<sup>dlc\*U</sup>, and *Cymatopleura* from the muddy bottom of the river (see similar case a<sup>t</sup> Burwell Lode, Dpwear, Cambs, Griffiths, 11, p. 120). The living m<sup>\*terial</sup>

\* See also Hinton, 14, p. 139. Local information in 1924 gWes rather lower limi\* <sup>of</sup> depth.

t Frequency is indicated as folW<sup>^</sup>-ccoabundant.cc.^comino<sup>^</sup>c<sup>^</sup>& Wy common, r.=a few, rr.arare, rrr.:=Tery rare.



*Holsatica*, *Chroococcus limneticus*, *Gloeotilia protogenita*, *Victyosp<sup>us</sup>*, *pulchellum*, *Richteriella botryoides* var. *tetraedrica*; rr. *Scenedesmus rf<sup>cauda</sup>*; rrr. *Surirella* (empty), *Pandorina Morum*, *Pediastrum<sup>B</sup>* *P. duplex*, *P. duplex* var. *rugulosum*, *Codastrum sph<sup>er</sup>icum<sup>q<sup>u</sup>US</sup>*, *quadrisseta*, *Chodatella Droscheri*, *Scenedesmus Hystix*, *S. opoliensis* var. *carinatus*, *S. Raciborskii*, *Tetraedron cauda un<sup>ncisum</sup>*.

GROUP B.—Norwich Area.

**Surlingham Broad.**

The Broad lies a short distance down the river Yare from Norwich, connected with the river by channels at both ends. Its area is about 100 acres, and the depth is not much over three or four feet. The surface of the Broad is spread with large islands of *Myriophyllum*, among the fronds of which are abundant masses of *Lemna gibba*, *L. poly<sup>triza</sup>*, and *L. minor*. A little *Hydrocharis* was also seen. The sides of the Broad are fringed with *Arundo*. The channels leading from the river to the Broad and the banks of the river itself, have a fringe of *Poa aquatica* and *Arundo*. There is a tidal rise of a foot or more in the river reported to go blue in summer, but not the Broad itself.

The phytoplankton of the Broad consisted largely of vegetable and epiphytic organisms from the submerged macrophyta. The following were noted:—cc. *Nitzschia acicularis*; c. *Cyclotella operculata*, *Ulna*; r. *Melosira varians*, *Fragilaria capucina*, *Oscillatoria chalybea*; rrr. *Pediastrum Boryanum*, *Scenedesmus cauda*, *Richteriella botryoides* var. *tetraedrica*.

**River Yare at Brundall.**

The collection was taken from the reach which runs parallel to the river. The collection contained much muddy detritus. The organisms which were present were very similar to those in the Broad, but in different proportions. c. *Nitzschia acicularis*, *Oscillatoria chalybea*; r. *Melosira variant*, *Ulna*; rr. *Cyclotella operculata*, *Actinastrum Ilantzschii*, *Scenedesmus cauda*; rrr. *Pediastrum Boryanum*, *Richteriella botryoides* var. *tetraedrica*.

**Rockland Broad.**

The Broad lies some distance down the river from Surlingham. It lies immediately at the foot of high ground at Rockland St. Mary. The headwater, and is connected with the river by a single outlet channel about three-quarters of a mile long. The area of the Broad is about a hundred acres and the depth some six or seven feet. The sides are fringed with *Arundo* and *Typha angustifolia*, with smaller amounts of *Scirpus lacustris* and *Sparganium*. Well out in the Broad are several small islands of *Arundo*. The bottom has large patches of *Potamogeton* sp., and the bays are well

*fyphir, Sippuris, and Sagittaria.* The water-level changes with the tide. It is reported locally that a few years ago the Broad was under-flooded with water and the fish were killed. The plankton contained much flocculent vegetable detritus, together with:—ccc. *Cydotella opereulata*; cc. *DuAyo-pherium pukhellum*, *Tetrastrum apieulatum* (*Crucigenia apiculata*); c. *A'terionella formosa*, *Pandorina Morum*, *Dinobryon Sertularia*; r. *Melosira* variant; rr. *Pediatrum Boryanum*, *Scenedesmus quadricauda*, *S. oblitquus*, *S. opoliensis* var. *earinatus*; rrr. *Melosira granulata*, *Pediastrum duplex*, *Tetratrum staurogenieforme*, *T. Bocklandensis*, sp. nov., *Lagerhetmta Wratisfaviensis*, *Aetmastium Hantzschii*, *Scenedesmus acuminatus*, *RyMenella* *Xiyoides* var. *tetmedrica*.

Ormesby Broad, near Yarmouth.

This Broad is the northern end of a large and much branched sheet of water which is called Bollesby Broad in its central part and Filby Broad at its southern end. The three sections are defined by two main roads which cross the Broad at narrow points where there are embankments and bridges. The whole Broad is a headwater, and is drained to the river by the Muckfleet at the southern end. The formation of the Broad was probably concurrent from that of the other (Pallis, 17, p. 220). The Broad is not tidal. At the time of collection, Ormesby Broad had a well-marked water-bloom of a blue-green colour. This is apparently normal for the season. The Broad was formerly used as a water-supply and, according to local information, the water had to be filtered twice. The area is about two hundred acres, and the depth from six to ten feet. Around the margin there is a sharply defined fringe of *Arundo* with fairly large patches of *Typhus angustifolia* and small masses of *Sagittaria laeustris*. Behind the rush-fringe on the north-east and north sides there is a wood of *Alnus* and *Pinus sylvestris*. The plankton was abundant and comprised:—ccc. *Melosira granulata*; c. *M. dextera*, *A'terionella formosa*, *Anabæna spiroïi*, *A. affinis*, *ApUmzcmenor* *Flos-aquæ*, *Gomphosperia lacustris*, *Mierocystis viruginosa*, *Pediastrum Boryanum*, *P. duplex*, *P. biradiatum*, *Dityospluznum* *r. M. opolis Flos-aquæ*, *Chroococcus hnetteus*, *Pediastrum Boryanum* var. *longicorne*, *Scenedesmus* **2** *Staurastrum dejectum*; *Pediastrum duplex* var. *clathratum*, *P. Kaw-Staurastrum tetracerum*, *Ceratium hirundinella* (two horned at base), *Viplopsalis* *Anabæna cirrifer*, *Limnermannii*, *Pediastrum duplex* var. *rugulowii*, *P. Tetras*, *Staurastrum carinatum* *S. ciborskii*, *Selastrum Bibraianum*, *Richteriella botryades* var. *tetraedna*, *Tottrum paradoxum*.

by the relative abundance of species and varieties of *Pediastrum*, as seen in Anting five microscopic fields, was;—iW <sup>TM</sup> *Boryanum* 14,

*P. Boryanum* var. *longicorne* 8, *P. duplex* var. *rugulosum* <sup>urA P duplex var.</sup> <sup>1.15(S)</sup>  
*daihratum* 3, *P. <?>ka?* 12, *P. Kawraiskii* 4, *P. biradiatum* 15. <sup>10-a1</sup>

#### THE DISTRIBUTION OF THE ALGA-FLORA.

The uniformity in the general level of the district, the <sup>f\*<sup>e</sup>V<sup>ient</sup></sup> <sup>F\*\*\*^d</sup> <sup>nce</sup>  
of both upper and lower connecting channels between Broad and river <sup>river</sup>  
the secondary tidal rise and fall of the fresh water, unite to bring <sup>about</sup> <sup>^</sup>  
association between river and lake which is not met with in other <sup>r parts</sup> <sup>^</sup>  
the English Lowland area. In this district there is a marked <sup>t y dency</sup> <sup>en</sup> <sup>^</sup>  
towards the intermingling of the moving-water habitat (kinetony <sup>dric</sup>) <sup>^</sup>  
the still-water habitat (statohydric), with a corresponding fusion <sup>between the</sup>  
respective potamo-and lacuplankton \*. The following table of <sup>the stations</sup>  
from which collections were taken shows the relation of the two na <sup>bitats :—</sup>

River Channels : River Bure above Wroxham Bridge; Kiver <sup>below</sup>  
Wroxham Broad; River Yare at Brundall.

Broads connected with the river by both upper and lower channels :

- (a) Shallow: Surlingham Broad. <sup>f9</sup>
- (b) Deep : Wroxham Broad ; " Upper Salhouse Broad.

Broads which are headwaters :

- (a) Shallow and tidal: Rockland Broad.
- (b) Deep and non-tidal: Ormesby Broad.

If the volume of the basin of the Broad is small in relation to <sup>the volume</sup>  
of river-water which flows into or through the Broad, the effect of <sup>f the river-</sup>  
water will be proportionately greater than if the basin of the <sup>DTOad was</sup> <sup>^</sup>  
greater volume—*e. g.*, Surlingham and Wroxham. Even <sup>in headw^ers</sup>  
which are connected with the river by single channels only, the <sup>tidal rise and</sup>  
fall may cause river-water to flow into the Broad—*e. g.*, RocJua <sup>nd Broads</sup>  
Ormesby Broad is without any tidal rise or fall, and the river effect, <sup>h for</sup>  
will probably be at its minimum.

The ecological meaning of the term " river " is obscure. Some of <sup>the chief</sup>  
features of rivers are given by Clark (4, p. 60 *seq.*). He says that <sup>t a river</sup> <sup>^</sup>  
from the point of view of the chemical composition of its water <sup>is</sup> <sup>^</sup>  
average of all the tributaries, plus rain- and ground-water. <sup>Ane smaller</sup>  
streams may be variable because of local conditions, but the large <sup>er rivers</sup>  
tend to resemble one another very closely, especially in their lower <sup>courses</sup> <sup>^</sup>  
The flowing river is well supplied with carbon dioxide from the air an <sup>d fro</sup> <sup>^</sup>

\* There is no term to denote the plankton of still water in general. <sup>i The term</sup>  
*lacuplankton* is suggested (*lacus*, *lacus*=pool, lake, basin of a fountain ; <sup>d g<sup>n</sup>ort,</sup>  
Latin Dictionary, Oxford, 1880). The writer has shown (Griffiths, 10) that the <sup>water</sup>  
plankton can be divided into the *limno-plankton* of the larger and deeper waters, <sup>the</sup>  
*plankton* of shallow waters, and the *heleo-plankton* of mixed or intermediate <sup>conditions.</sup>

the decaying vegetation. Its salts are abundant, and they are kept in solution by the carbon dioxide. Precipitation is rare.

It must, however, be pointed out that the rivers are of two distinct kinds. In the first group are those rivers in which the volume of water in the tributaries is greater than the volume of water which the main channel will hold. Here the water of the main channel is being constantly changed by the flow of the stream. This is the type of river to which reference is made above.

In the second group are those rivers which, owing to accidents of geological development, have beds which are too large for their present width with the result that the volume of the main channel is less than the volume of water supplied by the tributaries. Such rivers resemble greatly elongated lakes. The water in the main channel is not continually changed, and is like a long lake with a relatively small stream running through it. Rivers of this kind are really statohydric habitats and are only kinetohydric. They may, in fact, develop typical plankton of Myxophyceae, *Ceratium Urundella* and *Astmonella*. Ecology of the river may be a very variable habitat, and may vary in type from one part of its course to another.

The Bivers Tare and Bure in this district are lower courses, and they may be considered as showing the features which Clarke has described as great abundance of dissolved salts held in solution to a large extent by the plentiful dissolved carbon dioxide. They may be considered as kinetohydric habitats.

This habitat is apparently very unfavourable for most of the benthoplankton from the shallower weedy waters, but a few from the drainage area seem able to survive and form the so-called potamoplankton. Apart from casuals which have been swept into the stream by rain, all the remaining bedistinguishes two types of potamoplankton - a plentiful in the river as in the statohydric habitat, and a few in the shallower waters. In this area the *Opericula* (see West, 1915, p. 445) and *Richteriella botryoides*, *Tetrastrum apiculatum*, and *Scenedesmus optioides* are more plentiful than elsewhere may be.

represented by *Mdorira vanans*, which does not appear to be associated with weedy habitats through which run the large volumes of water (see West, 1915, p. 445) and the plankton of

ever Wuarfe, Yorks, describes what is perhaps a *notcenium*, which is more plentiful in the river than the other habitats. The rest of the wharf plankton appears to be more or less casual type.

The chemical effect of the river-water upon the water of the Broad will be to increase the salts-content of that habitat. Pearsall (W. 1913) pointed out the great influence of dissolved salts upon the periodicity of diatoms. As far as my experience goes, diatom abundance is also associated with considerable volume and depth of water, and high salts-content alone does not ensure diatom abundance. Shallow and weedy waters may have very high salts-content, but, nevertheless, there is no diatom abundance. Bytton Willows Pool, co. Durham, and most small lowland pools (Drew, 5). With this proviso, Pearsall's explanation may be applied to account for the immense abundance of *Melosira granulata* and *Attenella* in Wroxham and Ormesby Broads. This dominance is not found in the River Bure above Wroxham Broad, but only in the Broad itself and in the river Wrox, nor is it found in the shallow Rockland Broad. One might conclude that the significant ecological factors in this area are, first, a definitely limnoplanktonic habitat (*i. e.*, basins of some size and depth), and, secondly, enrichment of the water of the basin by the infusion of river-water, which contains much dissolved salts. The same explanation of the enrichment of limnoplanktonic habitats by the salts brought in by rivers may also account for similar dominance of *Melosira* in the Danish and North German waters described by Wesenberg-Lund (23).

The River Yare at Brundall might be considered to have a potamoplanktonic character in the sense given above. Its constituents are for the most part derived from the adjacent Surlingham Broad. *Omlatoria chalybea*, however, is more plentiful in the river than in the Broad, and may therefore be considered as having its origin in the river. The latter is contaminated with town effluent.

The plankton of the River Bure is also derived from still-water habitats, with the addition of the empty tests of diatoms from the mud. Below Wroxham Broad the river swarms with *Melosira granulata* and *Attenella* from the Broad.

Wroxham Broad itself, and "Upper Salhouse Broad," is limnoplanktonic, but greatly affected by the influence of the water of the river. There is a marked absence of Myxophyceae, *Attenella* is rare, the typical plankton of inland waters, *Ceratium hirundinella*, is not

Rockland Broad, off the River Yare, is mainly benthoplanktonic or heleoplanktonic, but the presence of certain Protococcales indicates potamoplanktonic influence.

Ormesby Broad is almost entirely limnoplanktonic. Myxophyceae are abundant, *Attenella* occurs in fair numbers and *Ceratium hirundinella* is also present. River-water influence is seen in the abundant occurrence of



*Melosira granulata* and *M. distans*. A peculiar feature of the plankton is the occurrence of several species of *Pediastrum* in considerable numbers. The presence of *Anabama affinis* and *Diplopsalis acuta* point to relation with continental waters rather than with other waters of the English Lowlands.

#### Relation to other Areas.

The plankton found in this area differs rather markedly in character from that encountered in other parts of the English Lowlands. Geographically, the area is not paralleled elsewhere in Great Britain, and it is necessary to turn to the Continent to find a similar district. In Denmark, perhaps, one finds the closest parallel to the conditions prevalent in this Norfolk area, and the plankton of the Danish lakes correspondingly resembles that found here. The other lakes of the English Lowland area are for the most part rather deep in proportion to their surface area, and their characteristic alga-floral dominants are Myxophyceae, *Asterionella* and *Ceratium hirundinella*. *Melosira granulata* only occasionally occurs, as in Hanmer Mere and in White and Chape Mere in the Shropshire-Cheshire district (Griffith, 8, p. 92), and also in Poper Bittell Reservoir, near Bromsgrove, Worcestershire, but never in abundance. The lake which most closely resembles the Broads in basin contour and depth is Hornsea Mere, E. Yorkshire, but this lake has a dominant Myxophycean flora together with a variety of *Ceratium hirundinella*. The significant geographical difference between Hornsea Mere and the Broads is the absence of river influence in the former, and this difference is shared by the other Lowland waters. It may be concluded, therefore, that the influx of river-water is the factor which differentiates this area from the rest of the Lowlands and equates it to the Danish area.

A peculiar feature of the Norfolk plankton is the absence of *Eudorina*. This alga has an extremely wide habitat range, and occurs in both neutral and alkaline waters and in all sizes of pools and lakes, and in very varied concentrations of dissolved salts. *Panhihrina* is more restricted in occurrence\* but nevertheless, the influence of river conditions seems to favour it, and it is characteristic "potamoplankton." *Eudorina*, however, appears to find the influx of river-water unfavourable to its growth, and its absence from the Plankton of the district is quite striking.

## List of Plankton Alga-flora.

	River Bur above Wroxbam Broad.	Wroxbam Broad.	River Bure below Wroxbam Broad.	"Upper Salbouse Broad."	Surlingbam Broad.	River Yare at Brundall.	Rockland Broad.	Oxmeaby Broad.
<b>BACILLARIUM.</b>								
<i>Cyclotella operculata</i> Kuetz. ....	∞	FTT	∞	∞	∞	IT	∞	∞
<i>Melastris varians</i> Ag. ....	∞	FTT	∞	∞	∞	IT	∞	∞
" <i>granulata</i> Ehrenb. ....	∞	CC	∞	∞	∞	IT	∞	∞
" <i>distans</i> Kuetz. ....	∞	CC	∞	∞	∞	IT	∞	∞
<i>Pragilaria capricornis</i> Desmaz. ....	∞	CC	∞	∞	∞	IT	∞	∞
" <i>Crotoneus</i> Kitton. ....	∞	∞	∞	∞	∞	IT	∞	∞
<i>Synedra</i> Uta Ehrenb. ....	∞	∞	∞	∞	∞	IT	∞	∞
<i>Asterionella formosa</i> Hass. ....	∞	∞	∞	∞	∞	IT	∞	∞
<i>Nitzschia acicularis</i> Kuetz. ....	∞	∞	∞	∞	∞	IT	∞	∞
<i>Synedra</i> sp. ....	∞	∞	∞	∞	∞	IT	∞	∞
<i>Gymnodonella</i> sp. ....	∞	∞	∞	∞	∞	IT	∞	∞
<i>Gamphyloides</i> sp. ....	∞	∞	∞	∞	∞	IT	∞	∞
<i>Gyrogonia</i> sp. ....	∞	∞	∞	∞	∞	IT	∞	∞
<b>MYXOPHYCEAE.</b>								
<i>Audouina circinata</i> (Kuetz.) Hantz. ....	∞	∞	∞	∞	∞	IT	∞	∞
" <i>Lemmermanni</i> P. Richter. ....	∞	∞	∞	∞	∞	IT	∞	∞
" <i>spiroides</i> Kleb. ....	∞	∞	∞	∞	∞	IT	∞	∞
" <i>affinis</i> Lemm. ....	∞	∞	∞	∞	∞	IT	∞	∞
<i>Oscillatoria chalybea</i> Mertens. ....	∞	∞	∞	∞	∞	IT	∞	∞
<i>Aphanizomenon flos-aquae</i> (L.) Ralfs. ....	∞	∞	∞	∞	∞	IT	∞	∞
<i>Gomphosiphon lacustris</i> Chod. ....	∞	∞	∞	∞	∞	IT	∞	∞
" <i>Nagehiana</i> (Unger) Lemm. ....	∞	∞	∞	∞	∞	IT	∞	∞
<i>Microcystis vinosa</i> Kuetz. ....	∞	∞	∞	∞	∞	IT	∞	∞
<i>Microcystis aquae</i> (Witttr.) Kirsh. ....	∞	∞	∞	∞	∞	IT	∞	∞
" <i>serica</i> Lemm. ....	∞	∞	∞	∞	∞	IT	∞	∞
<i>Chroococcoides nectens</i> Lemm. ....	∞	∞	∞	∞	∞	IT	∞	∞
<b>CHLOROPHYCEAE.</b>								
<b>ULONICHALINA.</b>								
<i>Glaciatia protogenita</i> Kuetz. ....	∞	IT	∞	∞	∞	IT	∞	∞
<b>PROTOCOCCALES.</b>								
<i>Pandorina Morum</i> (Muell.) Bory. ....	∞	ET	∞	∞	∞	IT	∞	∞
<i>Pediastrum Boryanum</i> (Turp.) Menegh. ....	∞	IT	∞	∞	∞	IT	∞	∞
" " var. <i>longicornis</i> Reinisch. ....	∞	IT	∞	∞	∞	IT	∞	∞
" " duplet Meyen. ....	∞	IT	∞	∞	∞	IT	∞	∞
" " var. <i>rugulatum</i> Racht. ....	∞	IT	∞	∞	∞	IT	∞	∞
" " var. <i>clathratum</i> A. Br. ....	∞	IT	∞	∞	∞	IT	∞	∞
" " <i>biradiatum</i> Meyen. ....	∞	IT	∞	∞	∞	IT	∞	∞
" " <i>Texas</i> (Ehrenb.) Ralfs. ....	∞	IT	∞	∞	∞	IT	∞	∞
" " <i>Kawaratskyi</i> Schmidt. ....	∞	IT	∞	∞	∞	IT	∞	∞

List Plants in *Alga-flora* O. ch.).

Plant Name	River Bure above Wroxham Broad.	Wroxham Broad.	River Bure below Wroxham Broad.	"Upper Salhouse Broad."	Surlingham Broad.	River Yare at Brundall.	Rockland Broad.	Ormesby Broad.
<b>CHLOROPHYTES (cont.).</b>								
<b>PROTOCOCCALES (cont.).</b>								
<i>Coelastrum sphaericum</i> Naeg. ....		G	F	HT			G	HT
<i>Tetrastrum apiculatum</i> (Lemm.) Schmidle ....							HT	
" <i>staurigeniforme</i> (Schroed.) Lemm. ....							HT	
" <i>Rocklandensis</i> sp. nov. ....							HT	
<i>Lagerheimia Wratistruvianis</i> Schroed. ....							HT	
<i>Chodatella Droebscheri</i> Lemm. ....		HT						
" <i>longisetia</i> Lemm. ....		HT						
<i>Actinastrium Hantzschii</i> Lagerh. ....		F				HT	HT	F
<i>Scenedesmus acuminatus</i> (Lagerh.) Chod. ....							HT	
" <i>byugatus</i> var. <i>alkermans</i> (Leinisch) Hansg. ....		HT						
" <i>denticulatus</i> Lagerh. ....		HT		HT				
" <i>Hypoxis</i> Lagerh. ....				HT				
" <i>obliqua</i> (Turp.) Kuetz. ....				HT				
" <i>opokiensis</i> P. Nichol (?) ....		HT		HT				HT
" <i>var. arinatus</i> Lemm. ....		HT		HT				HT
" <i>quadricauda</i> (Turp.) Bréb. ....		HT	3	HT				HT
" <i>Raciborskii</i> Woloszyńska ....		HT		HT				HT
<i>Ankistrodesmus falcatus</i> var. <i>mirabilis</i> W. & G. S. West ....		HT		HT				HT
<i>Selenastrum Hibernicum</i> Keinsch. ....		HT						HT
<i>Tetraedron minimum</i> (A. Br.) Hansg. ....		HT						HT
" <i>caudatum</i> var. <i>meissneri</i> Lagerh. ....		3						HT
" <i>limneticum</i> Borge ....		HT						HT
<i>Dictyosphaerium pulchellum</i> Wood ....		HT						HT
<i>Richterella botryoides</i> (Schmidle) Lemm., var. <i>tetradrica</i> Lemm. ....								HT
" <i>quadrata</i> Lemm. ....								HT
<i>Kirchneriella gracillima</i> Bohlin ....								HT
<b>ALGAE.</b>								
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## NOTES ON SPECIES.

**Bacillarie®.**

MELOSIRA (ORTHOSIRA) GRANULATA Ehrenb. (von Schoenfeldt, *Süßwasserflora*, 16). flora, Deutschlands, Osterreichs u. d. Schweiz, x. Bacillarieales, The diatom occurred in abundance in Wroxham and Ormesby association with *Melosira distans*. Under the name of *Orthosira punctata* n. sp., it is recorded by W. Smith in British Diatomaceae. n. P. "Ormesby, Norfolk, October and November 1853." It also occurs of the larger and deeper Lowland waters (Griffiths, 8, p. 82), and was by the writer in 192G in Upper Bittell Reservoir, a large and deep water near Bromsgrove, Worcs.

MELOSIRA DISTANS Kuetz. The dominant plankton in a co-dominant in Ormesby. Messrs. West record *AL crenidata* (= *JY. Binderiana* Kuetz., sec. von Schoenfeldt, *loc. cit.* p. 15) Neagh. *AL distans* differs from it in having no teeth on the valve face, in being less punctulate, and much broader and shorter.

**Myxophyce®.**

OSOILLATORIA CHALYBEA Mertens (Lemmerniann, *Kryitogamenflora Brandenburg, Hi., Algen I.* p. 3). Occurred mainly in River Brundall, and also in smaller quantities in Surlingham Broad. Its occurrence is probably due to a combination of sewage effluent and salt-water contamination.

ANABJSNA AFFINIS Lemm. *loc. cit.* pp. 179-183. Occurred only in Ormesby Broad. The variety *intermedia* Griff, is frequent in the of the larger waters of Southern Cheshire, Shropshire, and the Anglesey (Griffiths, 8, p. 91). The variety differs from the type only in

**Chlorophyceae.****Ulotrichales.**

GLOETILIA PROTOGENITA Kuetz. (Heering, in *Süßwasserflora*, vi. 50). Occurred in Wroxham Broad and Upper Salhouse Broad in some numbers. It resembles *Stichococcus scopulinus* Hazen in not having marked striations between the cells of the filament, but the size and form of the chloroplast equate it to *G. protogenita*.

**Frotococcales.**

PBDIASTRUM BIRADIATUM Meyen (Brunnthaler, in *Süßwasserflora*, p. 105). Common in Ormesby Broad, and found also in the River Wroxham Bridge. It has been found previously in Oss Mere, near church, Salop (Griffiths, 8, p. 8£). A typical specimen is shown as fig-

**PEDIASTRUM** KAWRAISKYI Schmidle (Brunnthaler, *loc. cit.* p. 103)..  
 This species occurred in some numbers in Ormesby Broad. It is peculiar  
 in having the prolongations of the peripheral cells of the coenobium arranged  
 transversely. It is a rare alga on the Continent, and does not appear to have

TEXT-FIGS. 1-4.

(The figures are drawings of *Pediastrum lucida*, at a magnification of  
 650 diameters.)

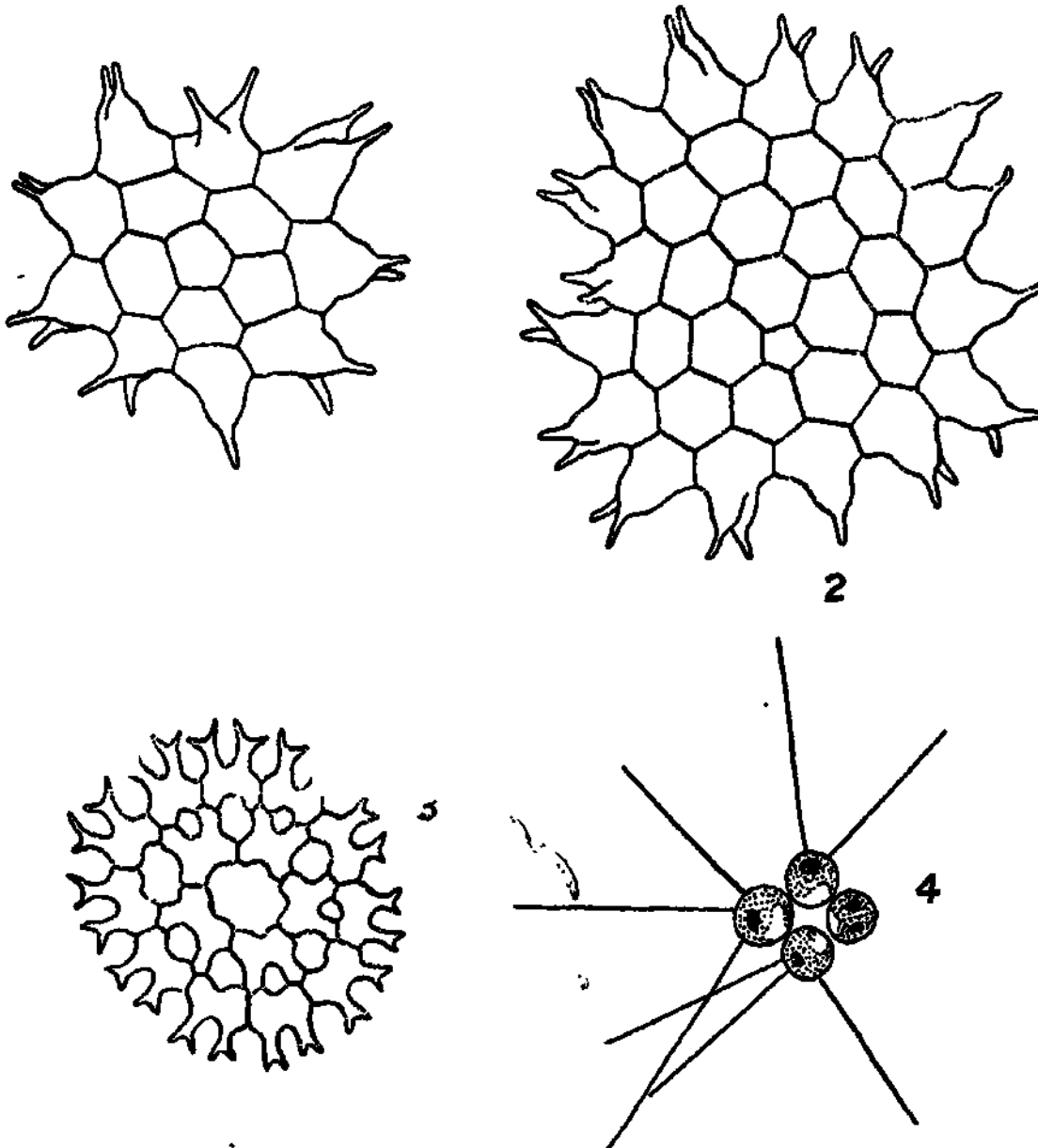


Fig. 1. *Pediastrum Kawraiskyi* Schmidle, from Ormesby Broad. Coenobium of fifteen cells.  
 Fig. 2. *Pediastrum Kawraiskyi* Schmidle, from Ormesby Broad. Coenobium of thirty-six cells.  
 Fig. 3. *Pediastrum bimidiatum* Meyen, from Ormesby Broad.  
 Fig. 4. *Rtoheteriella qundriseta* Lenim., from Upper Salhouse Broad.

been recorded for this country. It is widely distributed, and <sup>OC^AJ^B</sup> Wisconsin plankton in North America (Smith, G. M., 22, p. 1 <sup>1</sup> <sup>the</sup> <sup>pl. 46.</sup> figs. 10-13). Two specimens are shown as figs. 1 and 2.

TKTRASTRUM APICULATUM (Lemm.) Schmidle = *Staurogenia apiculata* (Lemm.) Lemm. (Brunnthaler, *loc. cit.* p. 177) = *Cmcigenia apiculata* Schmidle (Griffiths, Journ. Linnean Soc, Botany, vol. xliii. \*1916, p. pi. 34. fig. 13). The alga occurred in relative abundance in Broad. It has been recorded by the writer from Wilden Pool, under the name of *Crucigenia apiculata* (see above). supplied with water from the River Stour.

LAGERHBIMIA WRATISLAVIENSIS Schroeder. Also occurred Broad. It is rare, but widely distributed, having been found in 'Griffiths, 7, p. 9), Northumberland and Durham (Griffiths, Worcestershire (Grove, Bristol, and Carter, 12, p. 27), and on the (Brunnthaler, *loc. cit.* p. 13G).

CHODATELLA DROESCHERI Lemm. (Brunnthaler, *loc. cit.* Wroxham Broad, but very rare. It differs from *Ch. Droescheri* Lemm. in having the bristles distributed all over the cell and poles. It is apparently new to this country, but it is widely dis occurs in the Wisconsin plankton, U.S.A. (Smith, 22, p. 131, *Lage Droescheri* (Lemm.) Printz.).

OHODATELLA LONGISETA Lemm. (Brunnthaler, *loc. cit.* specimen seen in Wroxham Broad with six polar spines. It new to Britain ; it also occurs in the Wisconsin plankton.

SCENEDESMUS HYSTRIX Lagerh. (Brunnthaler, *loc. cit.* specimen seen in "Upper Salhouse Broad." The surface of adorned with very short hair-like processes. The record is new for this country. Again, it is also recorded for Wisconsin.

SCENEDESMUS OPOLIENSIS P. Richter var. *cannatus* Lemm. *loc. cit.* p. 166 ; Smith, G. M., 22, p. 159, pi. 41. figs. 8-11). rare, but widely distributed in the area, occurring in Wroxham and Ormesby. I have found U also in Battersea Park Pool, Ormesby one or two specimens were observed where the axes middle cells of the ccenobium were distinctly inclined obliquely, parallel, to the axes of the lateral cells, as in the type-form Brunnthaler, p. 164, fig. 228. All other specimens agreed with the and not with the type. Smith, however, figures the variety as These Norfolk specimens agree with his figures.

SCENEDESMUS RACIBORSKII Woloszynska (Griffiths, 6, p. figs. 7 & 8). This very curious species occurred in small Wroxham, Upper Salhouse, and Ormesby. The ccenobium was often

state of division (see figs. 6 & 7). It consists of a group of four slightly  
 lunated cells which adhere by their broad sides instead of by their narrower  
 edges. It differs from *Tetrademus wisconsinensis* G. M. Smith (Smith, 22,  
 P. 150 - 151; figs. 7, 11; also Brunnthaler, loc. cit. p. 160, footnote) in  
 Winer's reverse method of aggregation of the cells of the cenobium.  
*S. Raciborskii* not listed by Brunnthaler. I have found it in Wilden Pool,  
 Wrocks (see above).

TEXT-FIGS. 5-8.

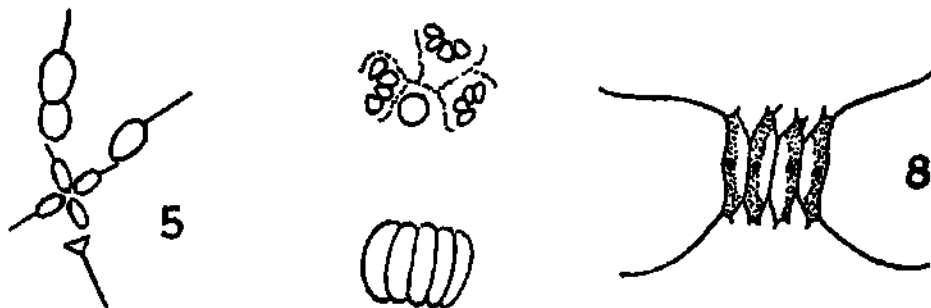


Fig. 5. *Tetrastrum Rocklandensis*, sp. nov., from Rockland Broad. Three cells of the  
 parental cenobium are figured, and the filial cenobium derived from the fourth.  
 Wrocks to the young cenobium there lies the spinous conical apical part of the

\* Fig. 7. *Tetrademus Raciborskii* Woloszynska, from Ormesby Broad. The figure shows an  
 axial view of a cenobium in which three of the cells are dividing. The young  
 cells are adhering by their lateral sides to form a packet.  
 Fig. 8. *Tetrademus opoliensis* P. Richter var. *carinatus* Lemm., from Ormesby Broad.  
 viewed laterally and posteriorly.

**Ric**  
*Ric* **HYPERIELLA BOTRYOIDES** (Schmidle) Lemm. = *Alicractinium pusillum*  
 (M. Smith, loc. cit. p. 125). The variety *tetraedrica* Lemm.  
 occurred in the Great Ouse Potamoc habitats in this area. The type was not seen,  
 but occurs in Ryton Willows Pool, Co. Durham, and is also recorded for  
 Wrocks by Hodgkiss (Groff, 3, 12, p. 27), Smith  
 says "the form *tetraedrica* (is) unworthy of recognition," but it seems  
 characteristic of this area, though doubtless it shades off into the type  
 elsewhere.

**Ric**  
*Ric* **HYPERIELLA QUADRISETA** Lemm. = *R. botryoidesvuwquadrisseta* (Lemm.)  
 Schudde (Brunnthaler, loc. cit. p. 119) = *Micractinium quadrisetum* (Lemm.)  
 G. M. Smith (Smith, loc. cit. p. 126). One specimen was seen in Upper  
 Chouse Broad (fig. 4).

**Desmidie**

**STAURASTRUM PARADOXUM** Meyen, var. *biradiatum* Griff. (Griffiths, Journ.  
 Lin. Soc, Botany, vol. xlvii. 1925, p. 89, pi. 1. figs. 1-3). This desmid is  
 quite characteristic of the larger and deeper Lowland waters. It appeared  
 in v. Wrocks Broad, but was not seen in Ormesby.

S. PARADOXUM Meyen and S. DEJECTUM Breb. were both seen in Ormesby Broad, the former in very small numbers and the latter rather more plentifully. Both are desmids of wide distribution.

Peridinieae.

CKRATIUM HIRDNDINELJLA O. F. Mueller. This characteristic plankton of the medium-sized and larger Lowland waters occurred only in Ormesby Broad. It is a rather small variety with only two basal horns, very much like the variety which was found by the writer in Hornsea Mere, Yorks (Griffiths, 9, p. 246).

DIPLOPSALIS ACUTA Entz. fil. (Schilling, in Süßwasserflora, p. 51) = *Glenodinium acutum* Apstein, in Das Süßwasserplankton, 1896, p. 152 = *Peridinium latum* Paulsen (Nordisches Plankton, viii. Peridinales, p. 41; also Lemmermann, loc. cit. p. 674, figs 1-7, p. 651). This very interesting

TEXT-FIGS. 9-11.

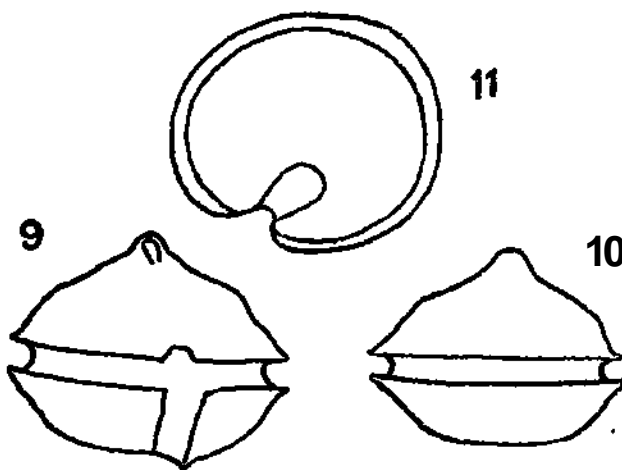


Fig. 9. *Diplopsalis acuta* Entz fil., from Ormesby Broad. Anterior view.  
 Fig. 10. " " " " " " " " Posterior view.  
 Fig. 11. " " " " " " " " Axial view, showing depth of the equatorial furrow and the oblique position of the longitudinal furrow.

Peridinium occurred in fair numbers in Ormesby Broad. It has been recorded for some of the North German lakes, but has not hitherto been found in this country. It is the only freshwater representative of a marine genus. It is shown in figs. 9, 10, 11.

TETRABTRUM ROCKLANDBENSIS, sp. nov. (fig. 5). One specimen of a species of *Tetrastrum* was observed in the plankton of Eockland Broad. It does not seem to agree with any form previously figured, and it is therefore described here as new. The colony consists of four ellipsoidal cells arranged in a cruciform manner. In the young coenobium the bases



Each cell has one apical axial spine, which is as long as or twice as long as the length of the cell. On division, the upper part of the wall of the cell appears to split off as a small conical cap with the spine projecting from the apex (see fig. 5). The diagnosis is as follows:—

*Tetrastrum Rocklandensis*, sp. nov. Ccenobium cruciforme, e quattuor cellulis ellipsoidalibus compositum; cellulae quaeque in apice spina axiali annata. Diam. cell. 5-6/\*, long. cell. 7-10/i; long. spinse 10-14/A.

Plankton Rockland Broad, Norfolk, England.

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Resin Canals in Seedling Conifers. By CHARLES S. HANES, Research Student of Downing College, Cambridge. Exhibition of 1851 Research Scholar. [Communicated by Professor A. C. SEWARD, F.R.S., F.L.S.]

(PLATE 37 and 20 Text-figures.)

[Read 12th May, 1927.]

The present account is concerned mainly with the primary resin canals of conifers, as distinct from canals occurring in tissues of cambial origin. Most of the observations have been made on seedling material, but where possible these have been supplemented by comparison with adult organs. In recent years considerable attention has been given to the resin-secreting structures in this group of plants: most investigators, however, have confined their studies to the resin canals in the secondary wood. The literature lacks comparative accounts of the primary resin canals, as most of the recorded data are incidental to the description of other features. It is hoped that the present account may help to fill in this gap, and give a more complete picture of the resin-secreting structures of the Conifers.

Some authors tend to emphasize the importance of the structure and distribution of resin canals as a clue to phylogeny. The writer hesitates to assign any such significance to the data on primary resin canals now presented. It is felt that much more must be known about the factors governing the secretion of resin before the character of resin canals can be interpreted as phylogenetic evidence.

Many species of Conifera have been examined, and I am deeply indebted to the many persons who have supplied material, especially to Dr. A. W. Seward, the Director, Royal Botanic Gardens, Kew, and to Mr. H. Ohlbert-Knecht, the Director, Cambridge Botanic Garden. I am also very grateful to Mr. T. G. Hill, of University College, London, who has been very helpful, and has kindly permitted me to use his extensive collection of serial sections of conifer seedlings. These preparations have greatly facilitated the work.

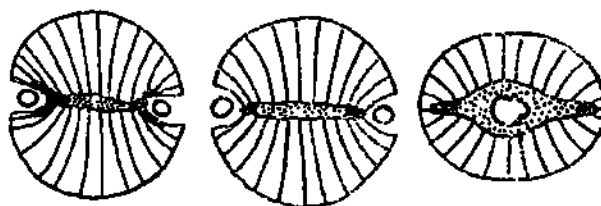
#### DESCRIPTION OF THE PRIMARY RESIN CANALS.

##### Tribe ABIETINEAE.

It has been known for many years that the Abietinae have primary resin canals in their roots. The canals are of two types, which will be referred to as the root-pole canals and the central canals. Root-pole canals are closely associated with primary xylem poles, and occur in the roots of the genera *Pinus*, *Podocarpus*, *Larix*, & *Picea*. If (\*\*\*)  $c_{TM}^h > o^H * \wedge \wedge$

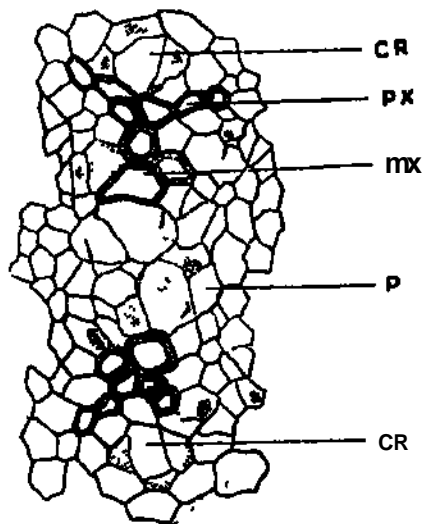
occur in the middle of the metaxylem, in the roots of *Abies*, *Cedrus*, *Pseudolarix*, and *Tsuga*. Van Tieghem (1872, p. 194; recognized these which are later referred to by Jeffrey (1905) when he proposed of the Abietineae into the two subfamilies Pineae and Abietese. shows the position of the two types of primary root canal.

TEXT-FIG. 1.



Roots of Abietineae, showing root-pole canals in A (*Pinus*) and B (*Pseudotsuga*); central root canal in C. In (*Picea*, *Larix*, and *Taxus*).

TEXT-FIG. 2.



Transverse section of a small root of *Pinus sylvestris*. (X 280.) CR, root-pole canal; PX, protoxylem; MX, metaxylem; P, undifferentiated tissue.

TEXT-FIG. 3.



Composite structure from the root-pole region of a *Pinus Strobus* root, (X280).

Root-pole canals lie close to the protoxylem plates of the root, and in the genus *Pinus*, where the protoxylem differentiates as a Y-shaped strand, a resin canal lies in the angle of the Y (text-fig. 1, A, and text-fig. 2).

the upper resin canal in text-fig. 2 a xy feature. Lrn in the same  
 W of the canal, which is an continuous wor dov m lly with  
 series of sections this \* y ^ w l a t T » 'uc ture is of the type nds  
 parenchyma cell. It is probable \* a \ ^ ^ were found. » ^ The  
 tissue from the region of the P<sup>11111111</sup> JJ<sup>a</sup> on containing 5 per cen  
 tissue was softened in an aqueous soi on g ghde.  
 and 5 per cent, chromic acid, and then teaseU ^ ra orophotog raphs 1 and 2  
 shown

Root-pole canals of older roots are  
 (P1. W)« . r in the u ^ ard extent of roo -P , 1 -lon g.  
 There is considerable vanahon m ^ extend up xnt o the P, o ^ ^  
 .Ufferent species: ^ ^ ^ gene Picea, i -JJ \* a P, o ^ ^  
 in other species of Pinws. » nd in ^ tn and root. 1« is shown in the  
 they end at lower levels in the hypocotyl

following table:-

<i>Pinus australis.</i>	The root-pole canals ex <sup>-tend</sup>	^ ^ ^ ttp the
<i>P. imignis.</i>	cotyledons.	of the cotyledons.
<i>P. ea;ce^a.</i>	The root-pole canals end in the upper region of the hypocoty^	
<i>P. Strobus.</i>		
<i>P. hahpensis.</i>		
<i>P. maritima.</i>		
<i>P. Coulteri.</i>		
<i>P. pinea.</i>	in the lower region of the	
<i>P. Gerardiana.)</i>		
£ < - < .		
<i>Picea.</i>	hypocoty	
<i>Pseudotsuga.</i>		<i>D. nodularis</i> the roots nave in

In the *gma AUes*, ^ ^ £ V ^ J K \*  
 primary resin canals of the cen ral o \* J 7 \* the descr iptions of the p  
 distribution, and xvill be mentioned  
 species.

Genus PINUS.0

PINUS AUSTRALIS.  
 Serial sections of two seedling\* "In the figure, canals fro node ^ ^  
 has a root-pole canal (text-fig- ^ er & t the cotyledoj undergo wrions,  
 cotyledons are shown joining to 6 ^ trands of ^ y ^ (1908) sngges t  
 one root-pole canal. The vascular ^ ^ ^ de jra ne I vascular gt rum  
 transitions in their course into fe ^ 10 o - t le Jo n is o ^ ^ a half-co,yledon  
 the following terminology : a j h o l e - c ^ t u r e (text . ng . 5),  
 descends to form one pole of the root

TEXT-FIG. 4.

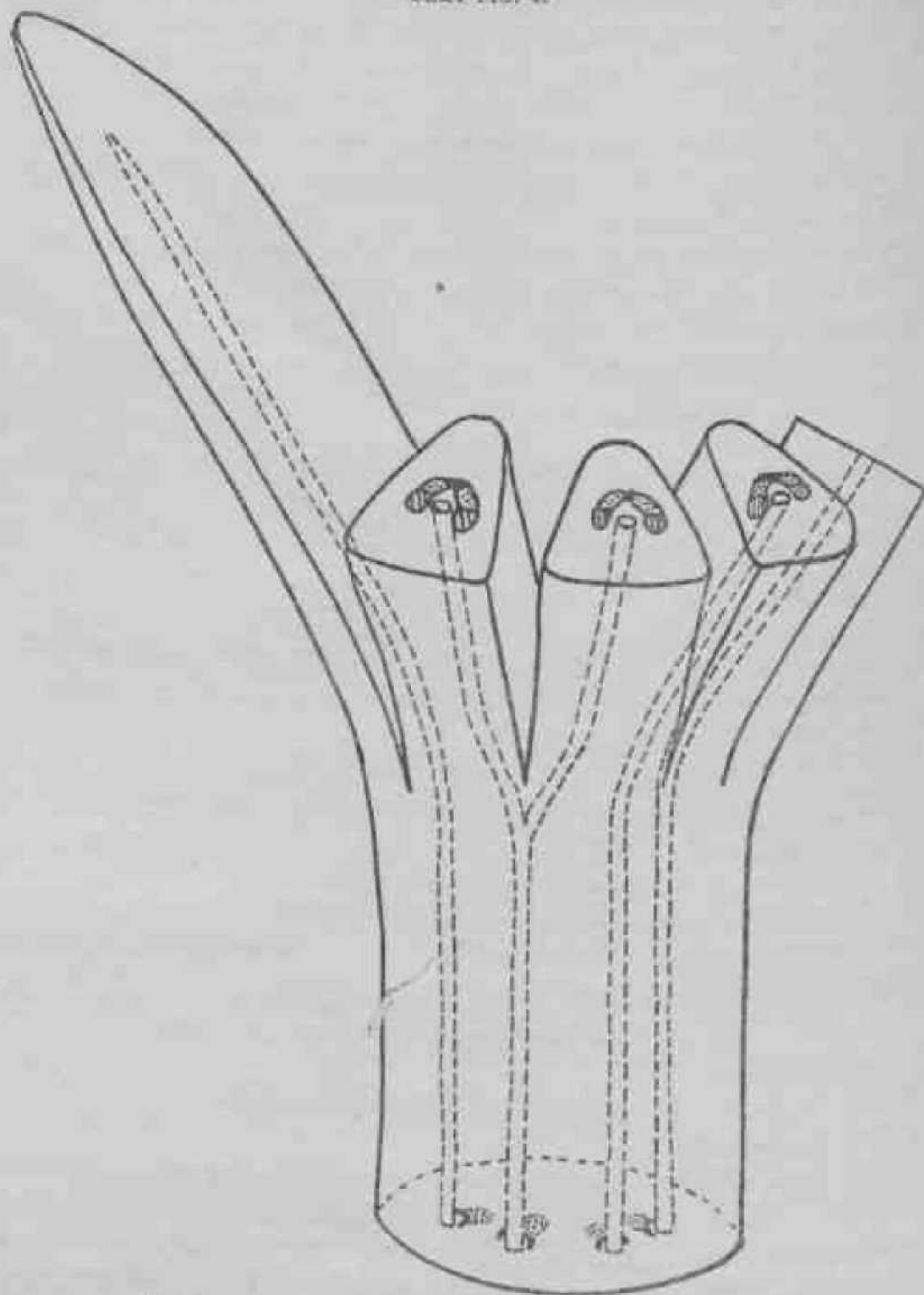
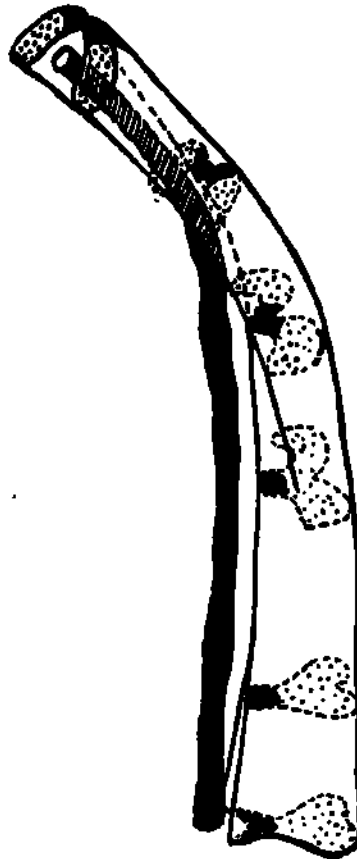


Diagram showing the cotyledonary node in *Pinus australis*.  
The root-pole resin canals are shown in dotted lines.

is one whose vascular strand corresponds to only one-half of a root-pole, in which case the root-pole bundle is bifurcated, a branch going to each of two adjacent half-cotyledons; the vascular strands of some cotyledons take no part in the formation of the root structure, and these are called subsidiary cotyledons. The half-cotyledons of *Pinus australis* possess branches of root-pole canals, as in text-fig. 4.

TEXT-FIG. 5.



Di

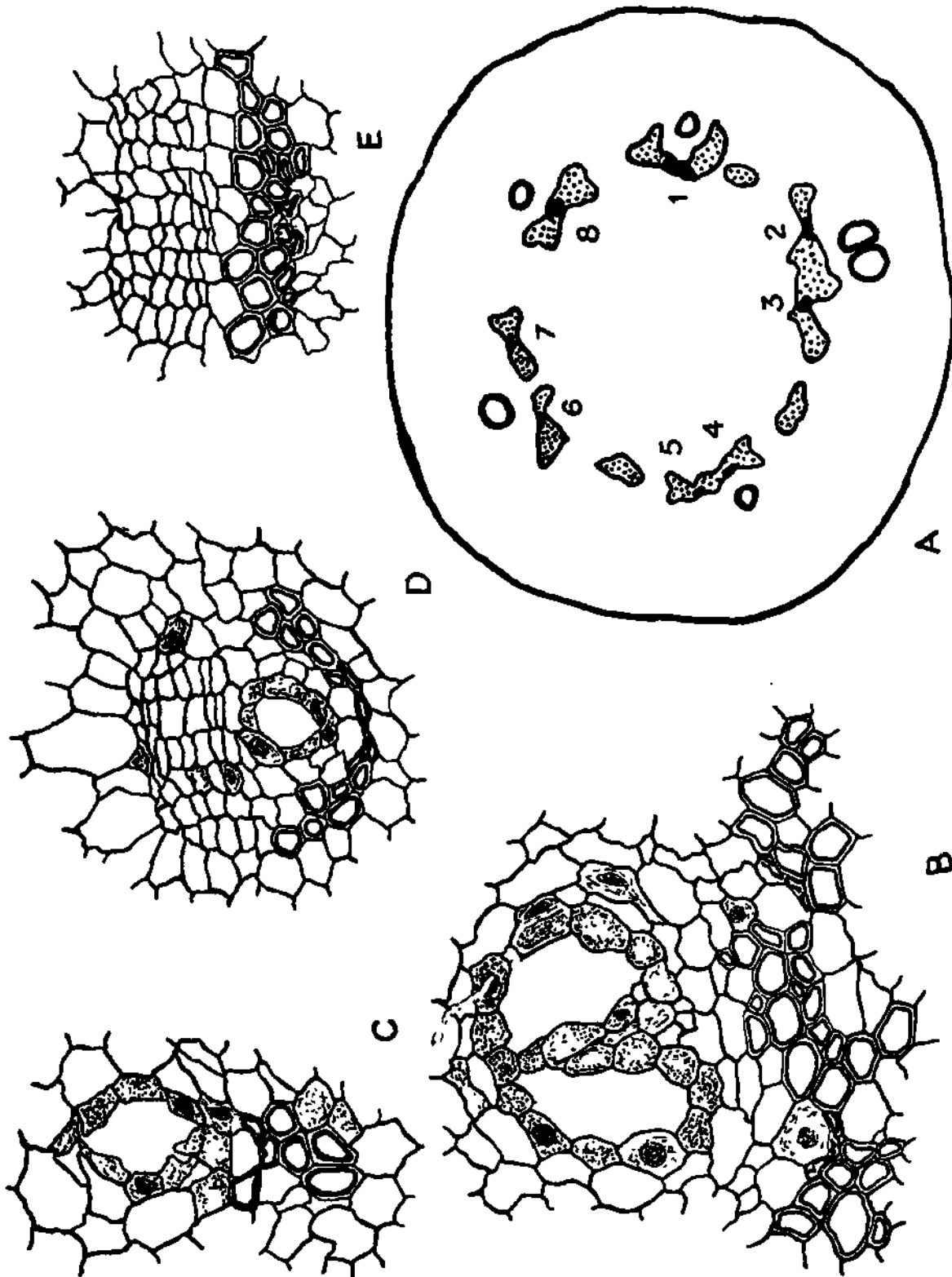
the root and the endarch in the cotyledon-  
protoxylem black; metaxylem dotted.

on region between the exarch structure in  
The root-pole canal is shown in black;

## PINUS INSIGNIS.

Text-fig. 4 will also serve for this species. Two seedlings were studied. One had five whole-cotyledons, each of which had a root-pole canal. In the other seedling there were eight cotyledons (text-fig. b, A). Numbers 1 to 8 in this diagram represent the vascular strands of the cotyledons. Nos. 1 and 8 are whole-cotyledons, and all the others are half-cotyledons. Nos. 1 and 8 have root-pole canals except No. 5. Other drawings show vascular strands with associated root-pole canals at different levels in the seedling.

## TEXT-JIG. G.



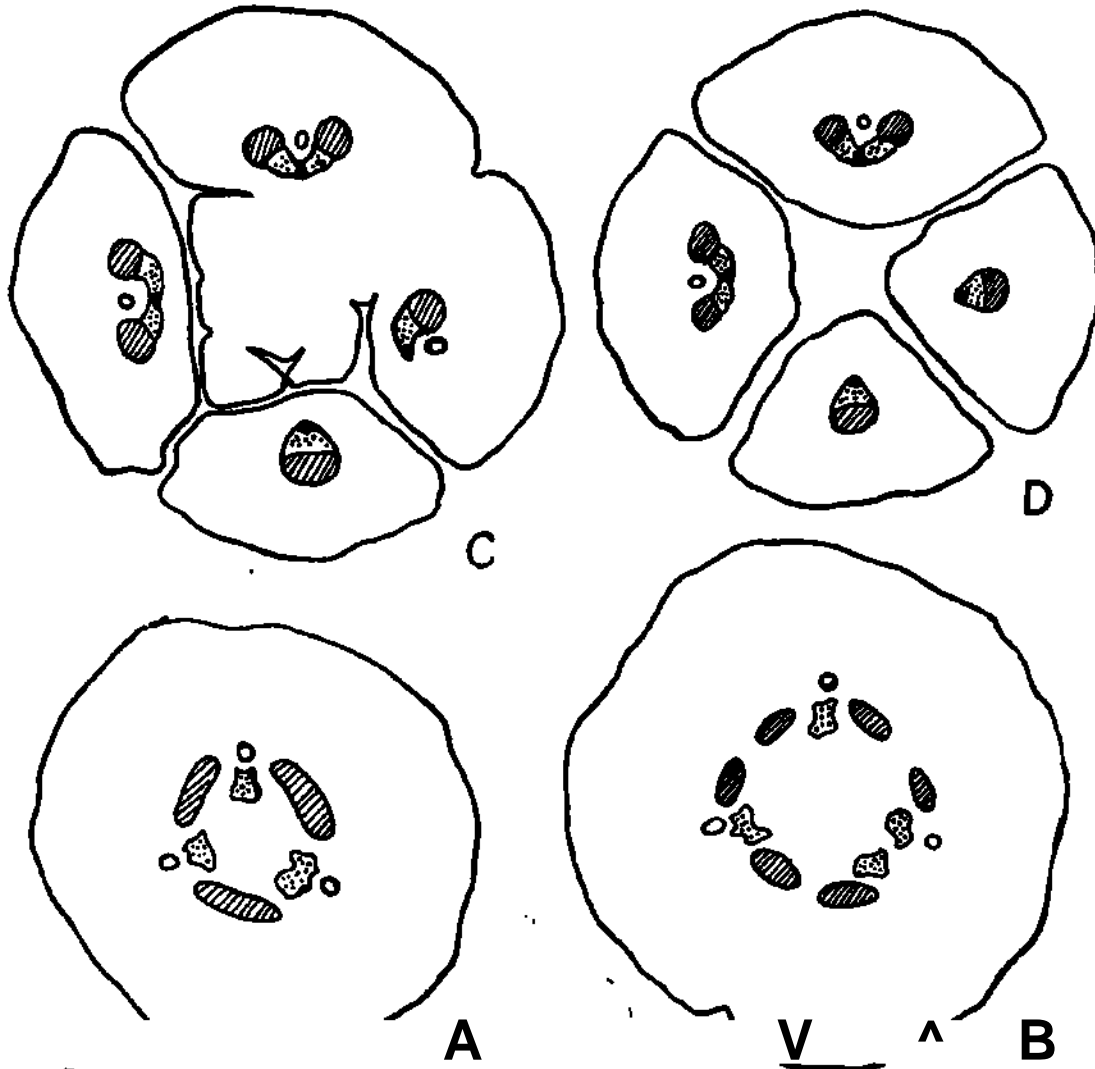
*Pinus inngnis*. A. Diagram of transverse section of cotyledonary node. Nos. 1-8 are cotyledonary traces. 1 and 8 are whole-cotyledons; all the others are half-cotyledons. B, C, D, and E show vascular strands (x 250). B, level of cotyledonary node; C, in lower part of hypocotyl; D & E, halfway up cotyledons 4 and 5. (No. 5 has no root-pole canal.)



*Pinus murrayana* (var. *Sargentii*).

Seedlings were used whose cotyledons varied from three to five in number. In four seedlings all the cotyledons were whole-cotyledons, and in these root-pole canals extended up about one-quarter of their length. The other seedling had two whole-cotyledons and two half-cotyledons (textfig. 7).

TEXT-FIG. 7.



*Pinus murrayana*. Sections at various levels (X 30). A, lower hypocotyl; B, upper hypocotyl; C, cotyledonary node; D, slightly above C.

In both species the root-pole canal extends to the tip. The smaller of the two half-cotyledons has no root-pole canal, while the larger one has only a short canal.

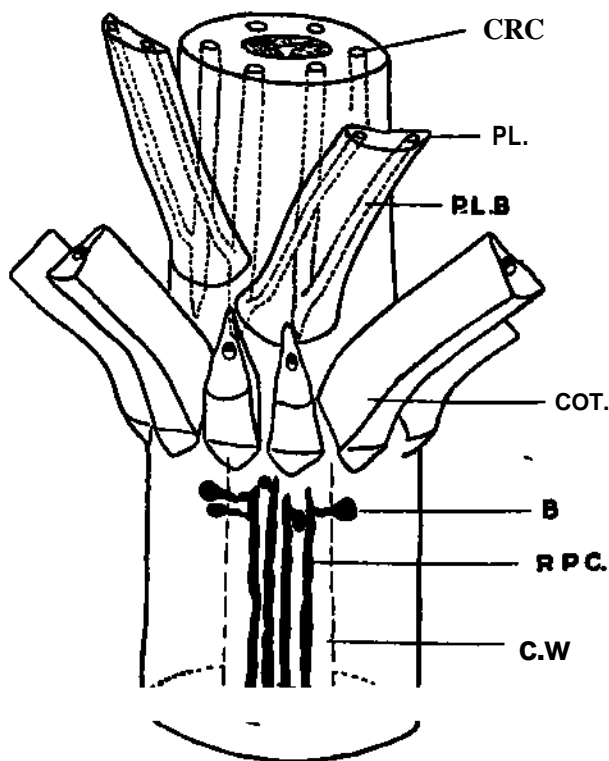
*Pinus sylvestris*.

Hill and (de Fraine (1909) and Chauveaud (1911) have described the vascular anatomy of this species, and have recorded the presence of short resin canals in the bases of the cotyledons. These short root-pole canals are absent from half-cotyledons.

PINUS EXOELSA, P. SIROBUS, P. HALEPENSIS, P. MABITIMA, and P. COULTERI.

These species have no canals in their cotyledons. The root-pole canals end in the upper part of the hypocotyl, as is shown in text-fig. 8. This diagram is based on *Pinus exceha*. At their upper ends the root-pole canals have numerous horizontal canals associated with them leading out to bulb-like expansions beyond the cambium. These structures were also observed in *P. Strains* and *P. maritima*, but the available seedlings of *P. halepi»\** and *P. Coulteri* were too young to show them. Those horizontal canals are

TEXT-FIG. 8.



*P. e.*  
 ^ r e ^ c ^ T i t h ^ n ^ C o t y l e o n a r y n o d \* - i t h e p i c o t y l . T h e r o o t - p o l e c a n a l s ( R \* < > \* > > > ) ( B ) o u t s W e t . r i z o D e t e l C a n a l s A t h e i r U P P < < " d . T h e h o r i z o n t a l c a n a l e r f \* e x p l a i n e d £ | £ C a m b i U m ( C < < ^ C O T ; c o t y l e d o n . C . R . C , P . L . , P - ^ B , " "

embedded in medullary rays and they connect openly with the root-pole canals. The bulbs are torraed from the cambium, and as they develop are i" Photomiorom-n^ P n n i a i , 7 C o r t e x . Several of these structures are sho"i" canals originatn?!" d 4 ( P h 37 > - . T h e y s e < < T M similar to the h e r i z o n t a l and roots, as descri!!7 t h J e r t i c a l canals in the secondary wood c f stems to these horizontal cana I h o i n s o n a Q d S i f t o n ( 1 9 2 5 ) . F u r t h e r r e f e r e n c e discussion. cana 1 9 o n d i n g 8 i n b u l b s i s m a d e l a t e r i n t h e c o n c l u d i n g

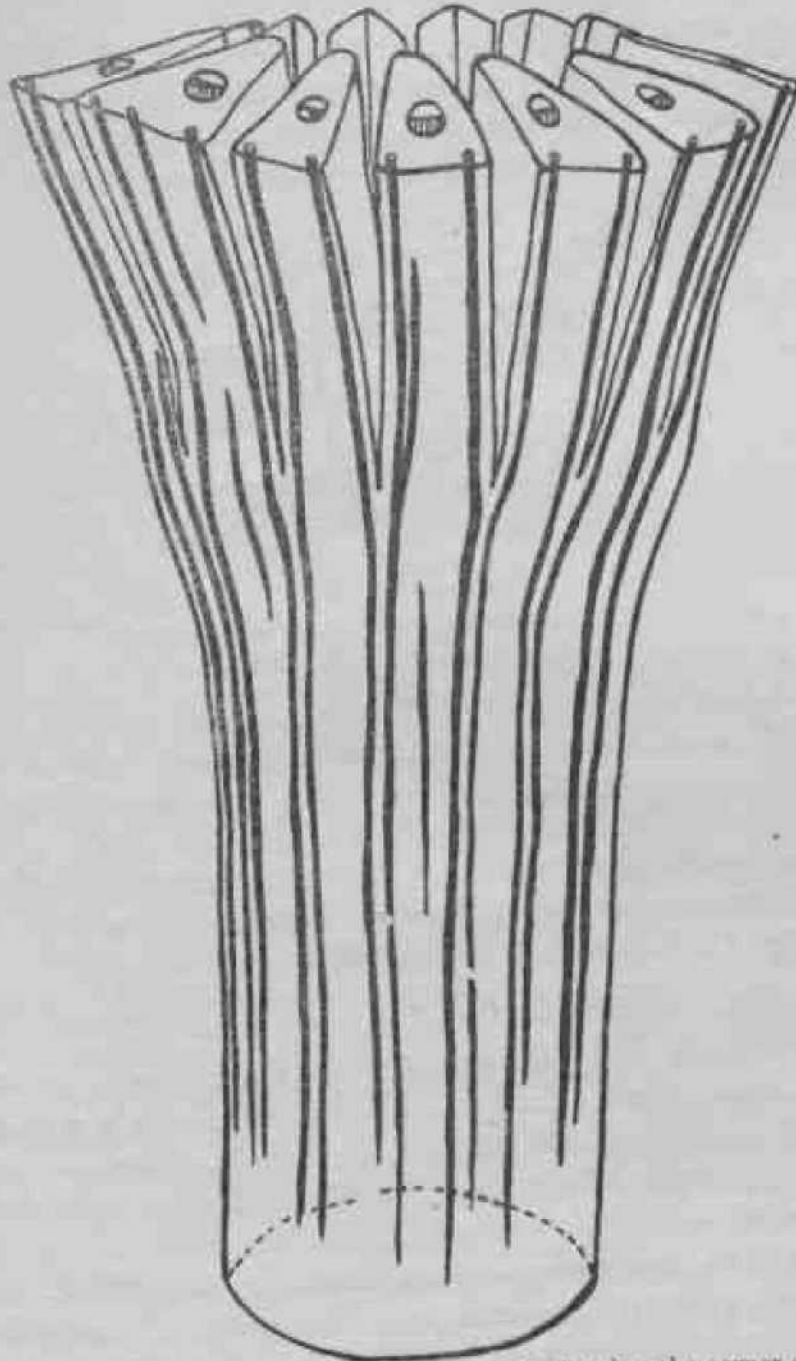
PINUS PINEA P n

The c o t y ^ ' S . T " " " \* ^ ' Q T M ^ k T M ^ and P " E D U " S - other resin canals l y n g - S 6 s p e C i e S h a v e n o r o o t - p o l e c a n a l s , b u t t h e r e a r e to as corner canals. \* \* m o r e s u p e r f i c i a l p o s i t i o n w h i c h w i l l b e r e f e r r e d

## PINUS PINEA.

About sixty seedlings of this species were obtained. Serial sections were made of six of these; the rest were observed under the binocular microscope, which reveals the course of the corner canals. Each cotyledon has a pair of these canals, which lie close beneath the surface, one in each of the outer

TEXT-FIG. 9.



*Pinus pinea.* Diagram of the cotyledonary node showing the corner canals.

corners of the cotyledonary node. The tips of the canals tend to be united in pairs.

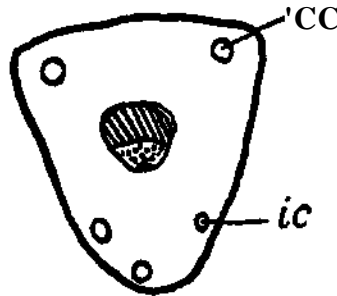
Many minor variations from the regular pattern occur, as is shown in text-fig. 9. In one specimen the two corner canals from adjacent cotyledons joined together and continued down the hypocotyl as a single canal. One small cotyledon had only one corner canal. Occasionally small additional canals are present, either as branches of corner canals or lying separately.

The canals develop at a very early stage, as was found from sections of » seedling still enclosed within the endosperm.

PINUS OANAMBNSIS.

This species also has corner canals which continue down the hypocotyl. In addition however, there are other superficial canals along the inner surfaces of the cotyledons. These are very short and do not continue into the hypocotyl (text-fig. 10).

TEXT-FIG. 10.



*Pinus canariensis*. Transverse section of a cotyledon, *cc*, corner canals; *ic*, canals along inner surfaces,

PINUS GEBARDIANA.

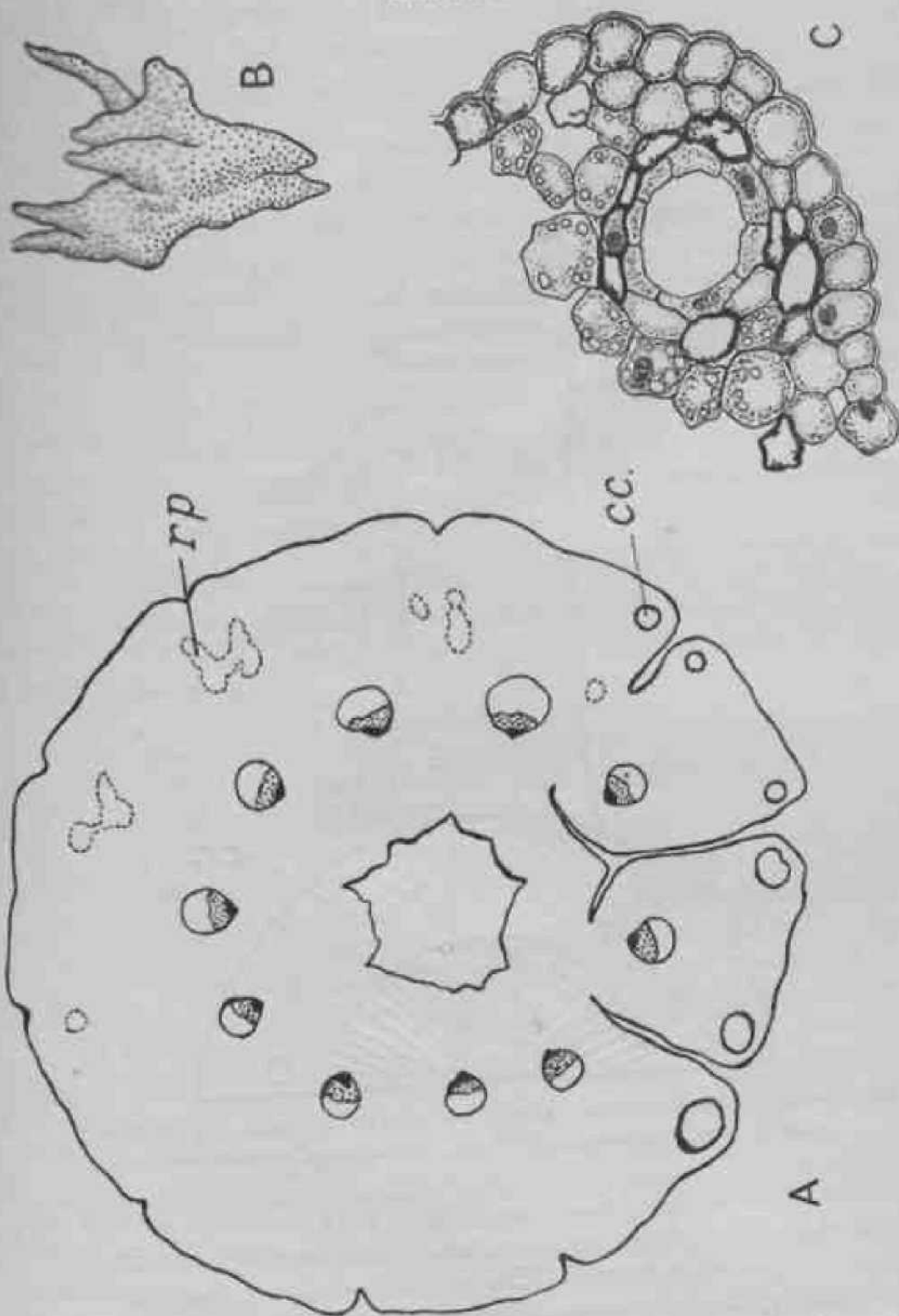
Twelve seedlings were sectioned. Corner canals are present, as in *P. pinea*\* but they end at the bases of the cotyledons, the hypocotyl having no cortical resin canals. Below the lines of junction of adjacent cotyledons there is a series of small cysts, or resin-pockets, shown in transverse section in text-fig. 11, A. A drawing of one of these, reconstructed from serial sections, is seen in text-fig. 11, B.

*The Stem and Leaves of Pinus.*

The epicotyl of a pine seedling is thickly covered with juvenile leaves arranged in a close spiral. Each leaf has two resin canals which lie in the mesophyll, one at each side of the vascular bundle. The position of these canals varies slightly in different species. The following description is based on *Pinus excelsa*.

The epicotyl, in transverse section, shows a ring of six conspicuous longitudinal canals. The leaf-traces pass out between them. At the base of each, juvenile leaf (P.L.) a branch canal (P.L.B.) of the two adjacent longitudinal canals of the epicotyl also continues out into the mesophyll. This is shown in text-fig. 8 and also in

TEXT-FIG. 11.

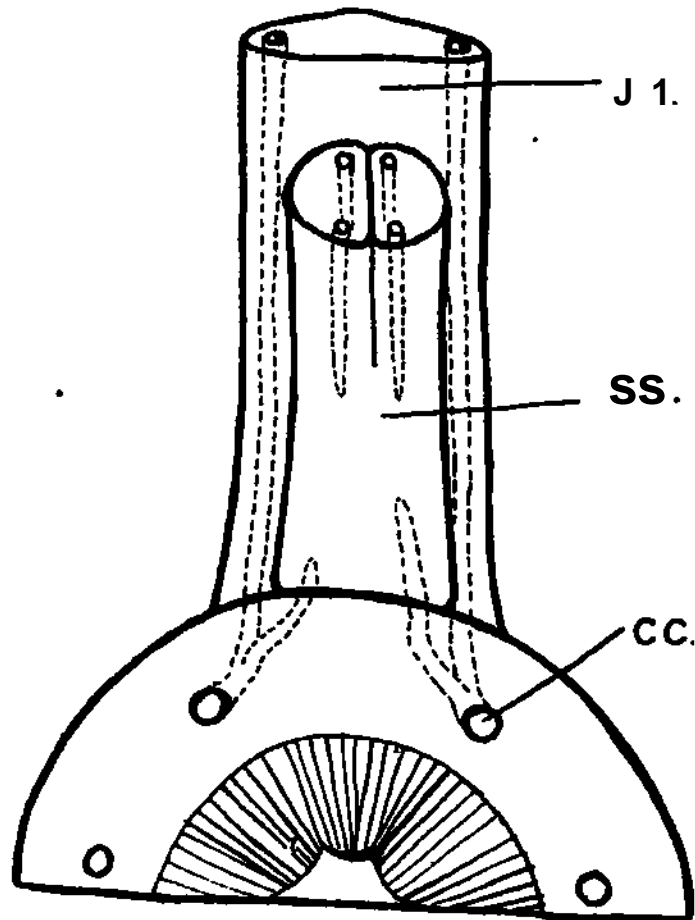


*Pinus Gerardiana*. A is a slightly oblique section through the cotyledonary node. cc, corner canals; rp, resin cysts. B shows a reconstruction of one of the cysts (rp). C, a corner canal ( $\times 250$ ). The dark cells without content are so-called tannin sacs.

microphotograph 5 (Pl. 37). In this section three longitudinal canals of the epicotyl are shown, with leaf-traces from two juvenile leaves between them: four smaller canals, the lateral canals of the two leaves, are cut in various stages of separation from the cortical canals.

The cortical canals of the epicotyl end blindly above the cotyledonary node. They do not connect with any lower resin canals. Moreover, the cortical canals of each year's growth in length form separate systems which do not connect with the canals in the cortex above or below. The number of canals which form in the cortex increases as the growing point of the stem becomes older.

TEXT-FIG. 12.



\*" ^r'sTurTot f \*", Di8eram of \* \* \* \* \* «a of a juvenile leaf.  
PM 8 h o o f ; > J u v e n i l e k a f ; c c , c o r t i c a l c a n a l o f y o u n g s t e m .

The resin canals in the adult leaves of « « • ^ve been dealt with by many investigators. The number and position of <>^ varies considerably in adult lives of £ same spec ... this is, however a tendency to be more constant than and in some species more prominent. The resin canals of pine needles have not been seen to connect with the cortical canals of the stem, even when spur shoots occur on very young stems in the axils of juvenile leaves. Such an instance is shown

in text-fig. 12, which is based on data from serial sections of a young stem of *Pinus Pinaster*. Short branches from the cortical canals run into the base of the spur shoot, but these do not connect with the adult leaf canals. The lateral canals of the juvenile leaf are connected with the stem canals, as was mentioned above. Spur shoots in *P. Strobus* and *P. Laricio* were similar.

#### Genus PICEA.

PICEA EXCELSA, P. AJANENSIS, P. NIGRA, P. MORINDA, and P. ALBA.

These are all similar in the distribution of resin canals. The cotyledons are small and have no resin canals. The root-pole canals do not extend above the root. In three-year-old plants of *Picea excelsa* and *P. Morinda* the upper endings of the root-pole canals were about two inches below the cotyledonary traces.

#### Genus LARIX.

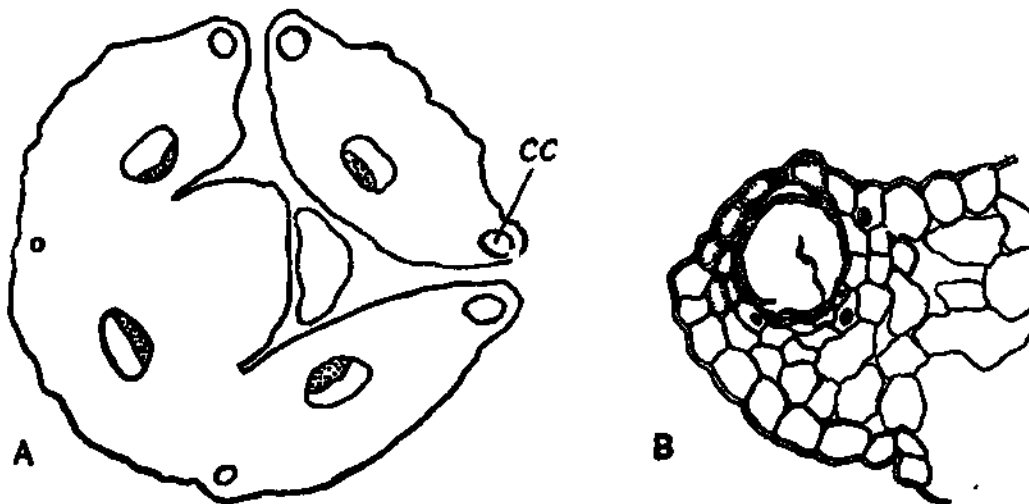
LARIX OCCIDENTALIS and L. LARICINA.

There are no resin canals in the cotyledons. The root-pole canals end in the lower part of the hypocotyl.

LARIX LEPTOLEPIS.

The two specimens examined had each four cotyledons, and in all of these there are short corner canals. The canals are very irregular and do not extend into the hypocotyl.

TEXT-FIG. 13.



*Abies bahamea*. A, section through cotyledonary node, showing corner canals, cc.  
B, a corner canal (X 250).

#### Genus ABIES.

ABIES BALSAMEA, A. VEITCHEI, A. NEPHROLEPIS, and A. MAGNIFICA.

In these species corner canals are present in the cotyledons. These canals do not extend below the cotyledonary node; they lie very close to the epidermis (text-fig. 13).

## ABIES SIBIRICA.

In the single specimen available there are corner canals \*s in the re-  
ceding species. There is also a series of cysts situated below the lines of  
junction of adjacent pairs of cotyledons as in *Pinus Gerardiana*\* These  
were not seen in any other species.

## ABIES PECTINATA.

There are no resin canals in the cotyledons, which are small.

## Genus CEPRUS.

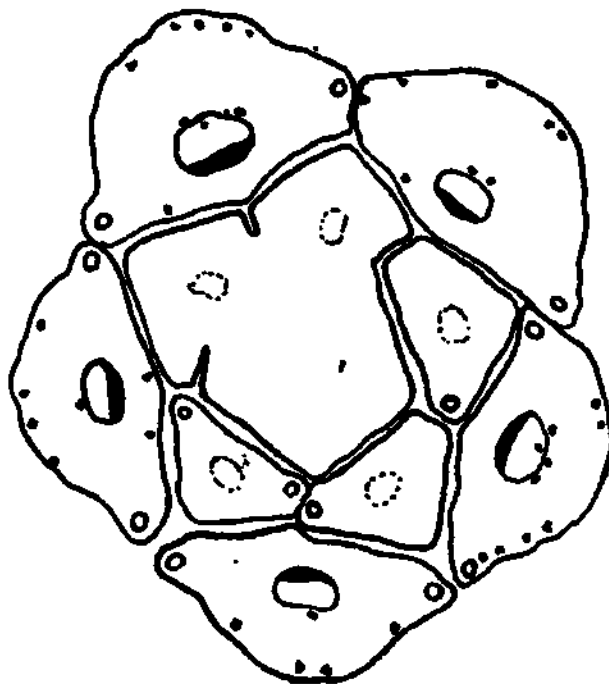
## OEDRUS DEODARA.

Two seedlings, each of which had eleven cotyledons, were examined. The  
extent of the canals in these is varied; some of the canals do not ex-  
higher than halfway up the cotyledon, while others are confined to  
upper part of the cotyledon.

## CEDRUS ATLANTICA.

No resin canals were seen in the cotyledons. Otherwise the seedling<sup>s</sup> are  
very similar to *Cedrus Deodara*.

TEXT-FIG. 14.



*Pseudolarix Kaempferi*. Section through cotyledons and leaves of the plumule.  
The small black dots represent tannin sacks.

## Genus PSEUDOLARIX.

## PSEUDOLARIX KAEMPFERI.

Two seedlings had each five cotyledons. Corner canals are present  
extending to the base of the cotyledons (text-fig. 14).

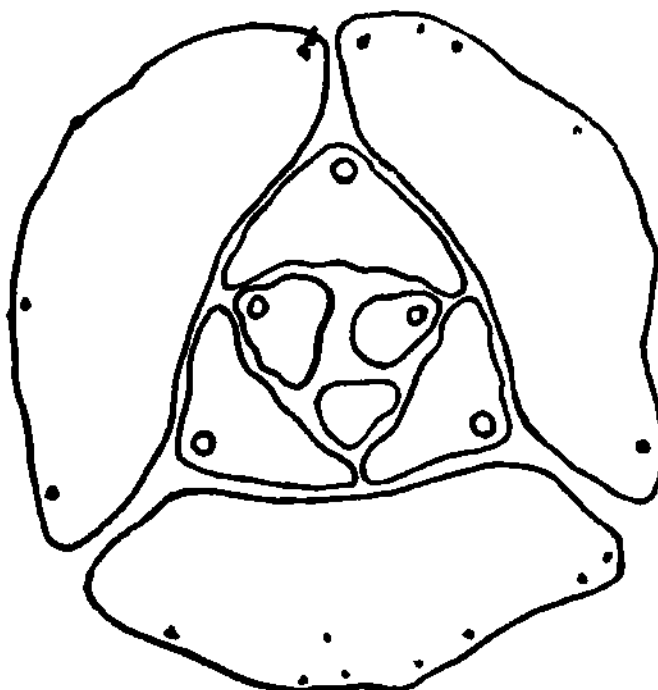


Genus *Tsuga*.

*Tsuga DIVESIFLORA* and *T. CANADENSIS*.

There are no canals in the cotyledons. The leaves of the plumule have a central canal which runs centrally beneath the midrib (text-figs. 15 & 16). These midrib canals extend down into the bases of the leaves, where they ena

TEXT-FIG. 15.



*Tsuga canadensis*. Section through cotyledons and plumular leaves. (Black dots are tannin sacks.)

Mindly. This is also the condition in adult leaves. Longitudinal cortical canals are not present in the stem. Thus *Tsuga* differs from the other *Abietineæ*.

Tribe CUPRESSINEÆ.

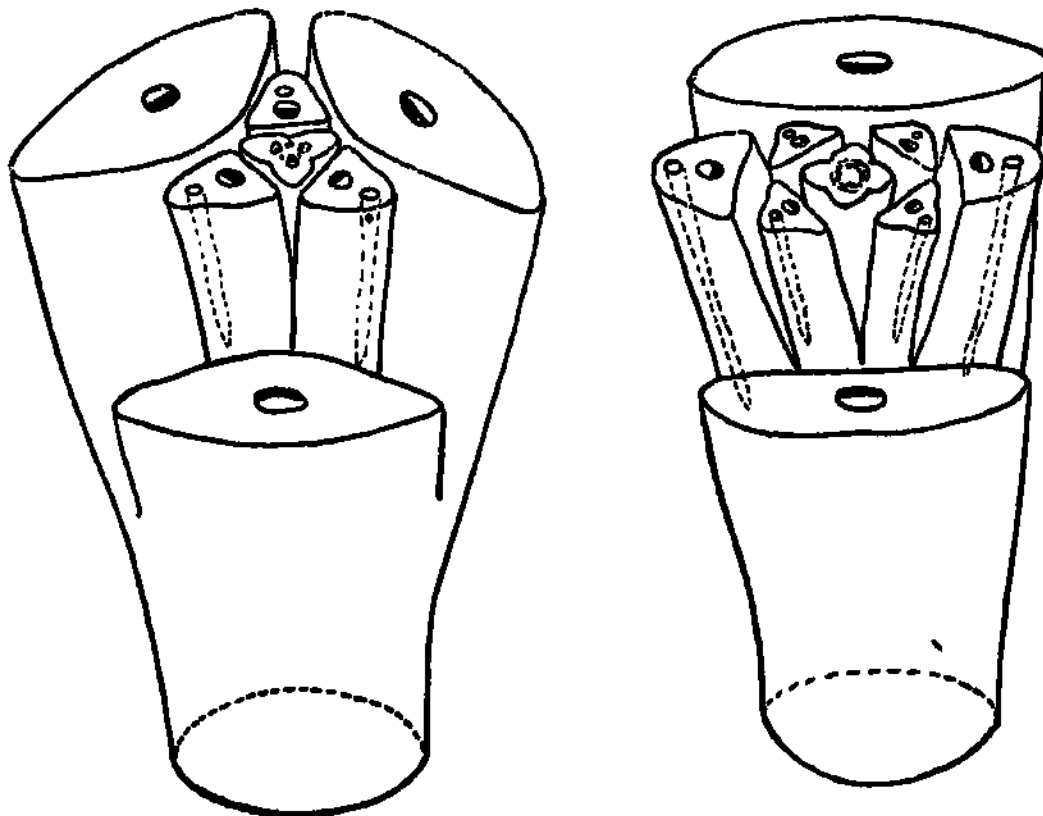
*Juniperus oxycedus*.  
 „ *berynudiana*.  
*Widdringtonia Whytei*.  
 „ *Mahoni*.  
*Actinostrobus pyramidalis*.  
*Thuja occidentalis*  
*Libocedrus decurrens*.  
*Cupressus Lawsoniana*.

*Cupressus torulosa*.  
 „ *obtusa*.  
*Callitris robusta*.  
 „ *verrucosa*,  
 „ *Afuelleri*.  
 „ *calcarata*.  
 „ *rhomboidea*\*  
 „ *australis*.

The distribution of resin canals in all these species is similar (text-fig. 16). It is the same as in *Tsuga*. (The adult leaves of many Cupressmean species

are very different in form from the juvenile leaves, and in these a corresponding difference is resin canal distribution occurs.)

TEXT-FIG. 16.



Seedlings of the Cupressinean type. Diagrams of the cotyledonary nodes of seedlings with two and three cotyledons.

### Tribe TAXODINEÆ.

#### CRYPTOMERIA JAPONICA.

Two seedlings were examined, each of which had three cotyledons. These contain a pair of corner canals ending in their bases. The hypocotyl has no resin canals. The juvenile leaves have not only corner canals which are short, but also midrib canals (text-fig. 17). The adult leaves are reduced and spine-like, and in these only the midrib canal is present, extending down into the leaf-base.

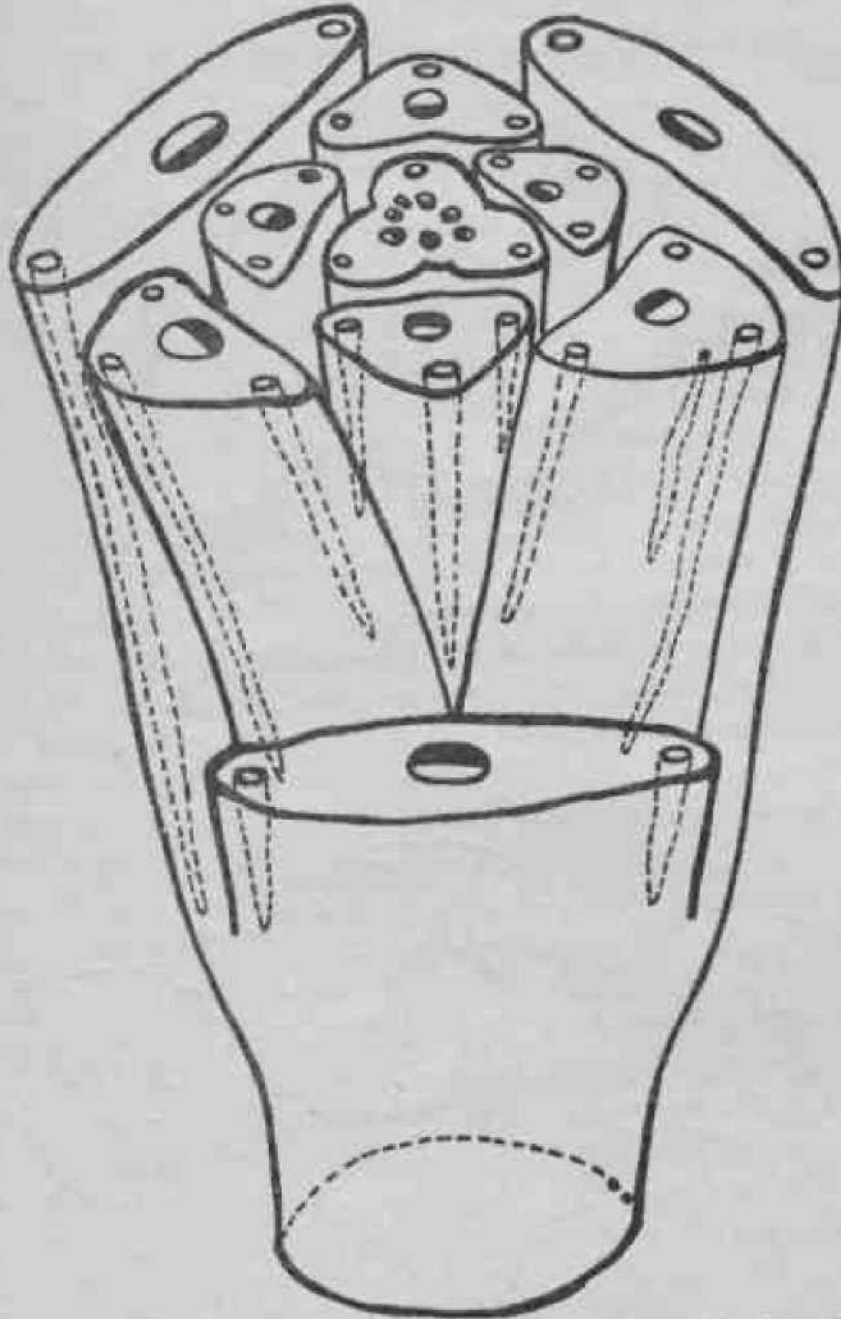
Leaves of the juvenile variety (*C. japonica* var. *elegant*) have both the midrib and corner canals as in the juvenile leaves of the seedling.

#### SEQUOIA GIGANTEA.

The cotyledons show a new feature. They have midrib canals which extend down to the lower part of the hypocotyl, where they end blindly. These canals are embedded in the cortical tissues, and are not comparable with the root-pole canals in the cotyledons of some species of *Pinus*. The juvenile leaves of the available seedlings had not yet developed resin canals,

as they w«« wry yarni\*. Adalt t\*»VM W\* simitr ro jfe cotyledons, having  
 canals in the midrib > sinon.

TEXT-FIG. 17.

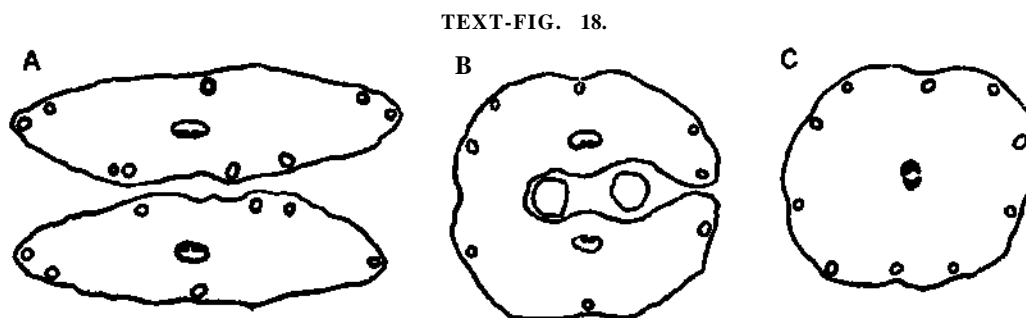


*Cryptomeria japonica*. Diagram of cotyledonary node showing cotyledons with corner canals; plumular leaves with corner and midrib canals.

Four seedlin... ledons which are broad  
 and flat. These have no raim tttuais. 1\*e jnv.ni^ lam\* h\_A» a....rib  
 canal, iiuliof in the Im^, Adult Imve\* h>vo Midrib CfdliO dnd oortior  
 canals. Tho bitUr nre v.rv short, and Uo dot continue d to Ot b^ of  
 the leaves.

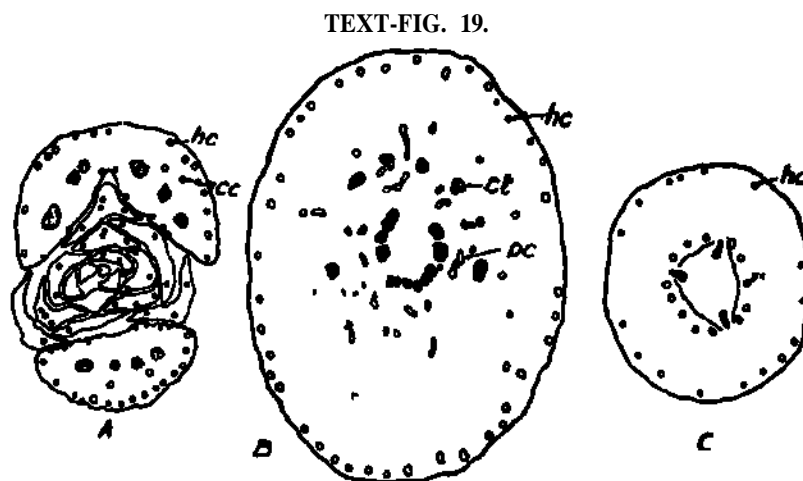
## SCIADOPITYS VERTICILLATA.

The seedlings have two broad cotyledons. Numerous superficial canals<sup>1</sup> are present along both surfaces (text-fig. 18). The canals of the inner surfaces are very short; the outer ones are longer, and some of them extend<sup>1d</sup> down the hypocotyl. Thus the hypocotyl has eight or ten superficial canals running to its base.



*Sciadopitys verticillata*. Sections at different levels of a seedling. A, lower part of cotyledons; B, at the cotyledonary node; C, halfway down the hypocotyl.

The juvenile leaves usually have three canals lying close to the epidermis in the midrib and corner positions. These are variable; sometimes there are as many as five such canals; there are often smaller ones along the inner surfaces also, as in the cotyledons.



*Araucaria imbricata*. Sections through seedlings. A, cotyledons and plumular leaves; B, upper level of hypocotyl; C, the root.

## Tribe TAXINEIE.

TAXUS BACCATA and T. CUSPIDATA.

Resin canals not present in these species.

OEPHALOTAXUS PEDUNCULATA, O. FORTUNEI, and C. DRUPACBA.

The distribution of canals in the seedlings is the same as in the Uupresrineie (text-fig. 16).



THE FORMATION OF RESIN CANALS.

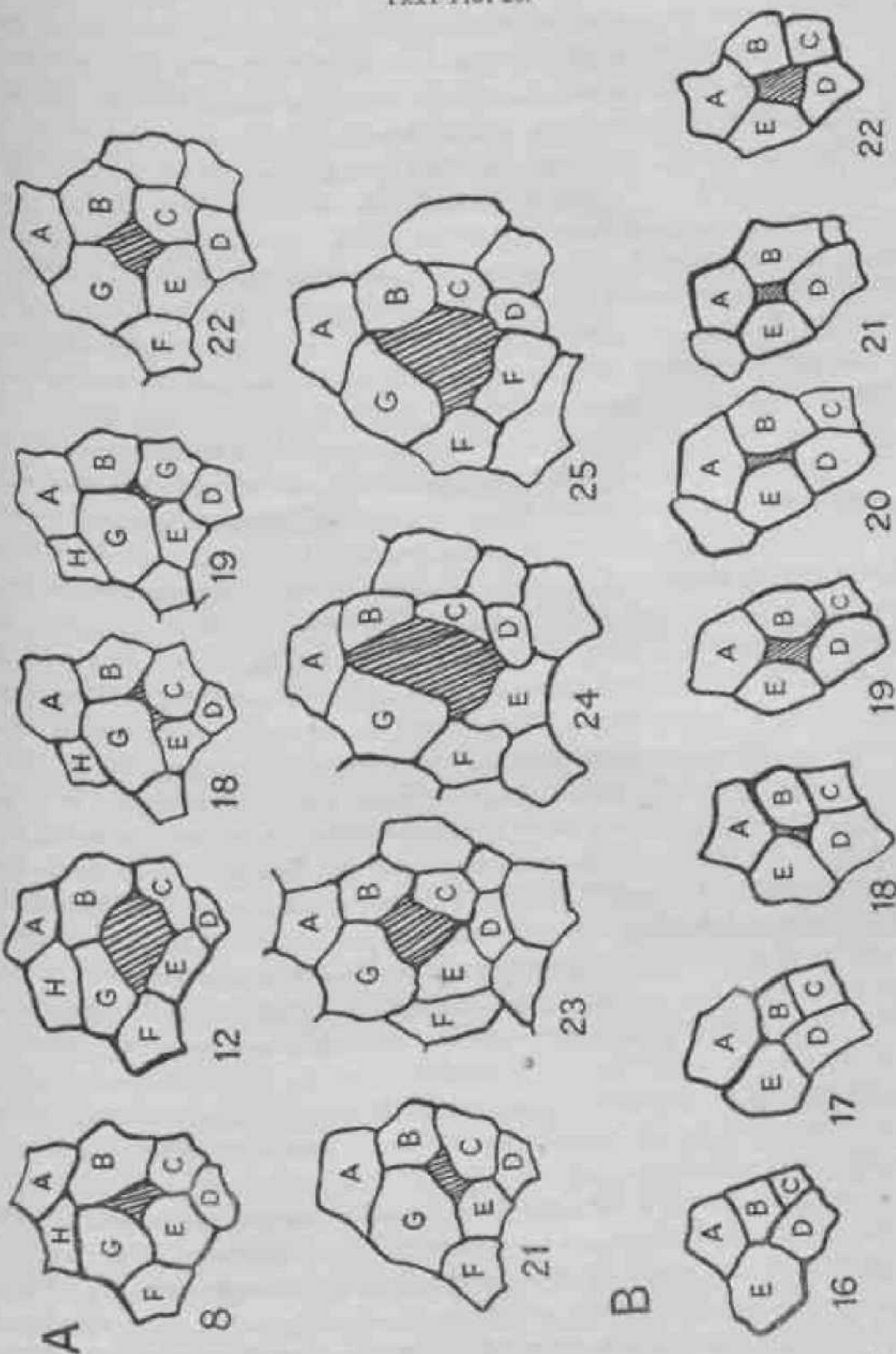
The resin canals which have been described, except those in *Araucaria*, are formed as intercellular spaces, and not by the breakdown of cells, at least in the young stages studied. The canals develop in the cotyledons of seedlings early in germination. In several seedlings these developing canals showed that actual cell-division was taking no part in the differentiation of the lumen. This is best explained by reference to text-fig. 20. The cells in these sections form a cord of tissue in which a resin canal is developing. The drawings are at different levels in a series of sections of the cotyledon of *Cedrus deodara*, and they are numbered in their order in the series. Cells of similar cross-section recur at successive levels. These are not sections of the same cell, but of cells of the same longitudinal row. It is evident that no cell-division has taken place in the change from a solid cord of tissue into the resin canal with a considerable lumen, since there are no interruptions in the arrangement of the cells in longitudinal serialiations. Consequently the prevalent conception that the formation of resin canals is due to cells dividing and pulling apart is inadequate. In the later development of resin canals there is often considerable cell-division, sometimes

arranging them into a many-layered sheath about the canal. Thomson and Sifton (1925) describe structures of this kind. Obviously, however, it becomes necessary to look for some new factor to account for the appearance of « lumen » in the young developing resin canal. It is suggested that the actual pressure of the fluid resin may play an important part in this differentiation. The corner canals in the cotyledons of *Pinus pinea*, even in very early stages, are filled with the secretion. This has been demonstrated by the method of Hannig (1922) in canals of *Pinus sylvestris* in which the method of Tolunski (1928) was used. In Hannig's fixative (1 per cent, chromic acid solution) the resin is washed out. In the protoplasm, even the canal walls are stained. It is evident, therefore, that the formation of the lumen of a resin canal is associated with the secretion of resin. It is suggested that the pressure of the resin of the cells to form

The existence of a pressure is easily demonstrated in such canals as the

\* T or less  
 prepared by adding a solution of copper salts of organic acids of more than 1 per cent concentration to a solution of ordinary washing-soap were precipitated, with the exception of those of the green colouring resin by the action of copper-acetate solution.

TEXT-FIG. 20.



*Cedrus Deodara*. Drawings from series of sections showing developing corner canals. The order in the series. Description in the text.

corner canals of a cotyledon of *Pinus pinea*. This is done by dissecting away under a binocular microscope the soft tissue surrounding a canal; the canal is then pricked with a fine needle. A drop of resin immediately forms at the puncture. This occurs in various stages of development. A more striking illustration is found in the blister-like swellings of the cortex of *Abies balsamea*. These blisters of resin are formed as swellings of the cortical resin canals. They become noticeable on the surface only on vertical parts of the stem which are at least five or six years old; the size increases with age, so that blisters an inch across are common on old trunks. These structures are very turgid at all stages; if they are punctured, there is an immediate flow of resin from the opening. It seems probable that the gradual accumulation of resin secreted into the lumen distends the walls of the canals at points of weakness.

The shape of a resin-containing structure is related to the grain of the tissue in which it lies. When the tissue is composed of elements elongated in one direction or arranged in longitudinal rows, then the resin lies in a canal running in the longitudinal direction. This is true not only of the primary canals, but also of the canals in the secondary wood and medullary ray.

Mention has already been made of the peculiar bulb-like structures in the bast which terminate horizontal canals from medullary rays. These horizontal canals may take origin either from the root-pole canals, as has been described in *Pinus*, or from vertical canals of the secondary wood. It is possible that these bulbs may be formed by the action of the resin secreted by the canals in the xylem. These cannot increase in volume owing to the firmness of the matrix about them, and consequently excess resin is pressed outwards through horizontal canals. Several stages in the development of these structures are shown in photomicrographs 3 and 4 (PI. 37). In the first the lumen of the canal is open across the cambial zone, and the resin is continuous from the root-pole canal to the bulb in the bast. (Thomson and Sifton have described these structures in *Picea canadensis*; they find that the lumen of the horizontal canal in older stems is often closed at the cambium. This is possibly because the vertical canals, from which the horizontal canals have come, may be old and the secretion of resin into them may have diminished or ceased.)

Up to the present it has not been possible to test experimentally the hypothesis which has been outlined above. The inadequacy of the current conception of the origin of resin canals has been demonstrated, and it is suggested that the pressure of secretion of resin may play an important part in the development of the resin-container. It should be emphasized that this is presented merely as a working hypothesis.



RESIN CANALS IN SBBDLIK8 CONIFERS.

THE EFFRCT OF WOUNDINS UPON THE PRODUCTION OF RESIN CANALS.

When the cambium of most conifers is injured, there is a great increase\* the number of resin canals in the subsequently-formed secondary wood. The work of Thomson and Sifton has demonstrated that even the so-called "normal" or scattered resin canals in the wood of *Picea* are traced to a cambial disturbance. This work suggests that traumaticism have an importance, hitherto unsuspected, in causing the differentiation of resin-secreting tissue from the cambium. In view of these results, it is desirable to investigate the effect of wounding upon the production of primary resin canals.

A number of experiments were carried out in which growing points were objected to wounds of varying severity; several types of material were used: growing root-tips of *Larix laricina*, stems of *Abies balsamea*, *M. glauca* and young cotyledons of *P. pinea*. The wounds were effected by Pinching with forceps; pricking with needles, etc., and were produced marked effects upon the cambium of these species. The material was collected and compared with unwounded controls, in which no significant differences in the presence and number of primary resin canals.

It seems that the canals of primary tissue are not induced by wounding, as is so strikingly the case in canals of the secondary wood. The effect of wounding may be more apparent than real. The secretion of resin takes place only within parenchymatous tissue. This is true of the canals of the secondary wood; these often form a branching network of passages within a mass of parenchyma. In the experiments on growing points mentioned above, there was no abnormal development of primary resin canals. Wounding of the cambium, on the other hand, causes an interruption of the normal flow of elements, which would normally become traces, and so the effect of the wound is to increase the amount of parenchyma in the secondary wood, with a consequent increased secretion of resin.

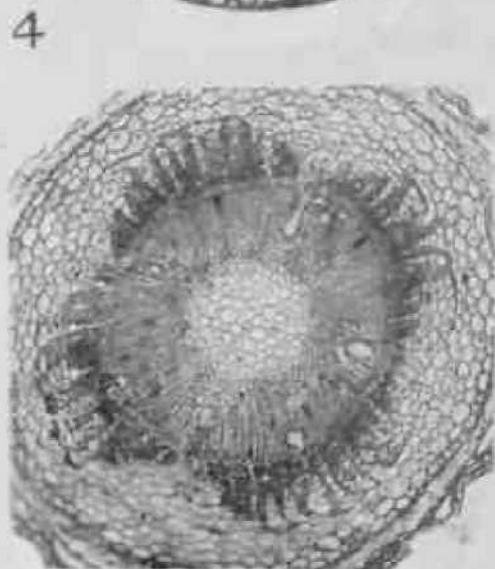
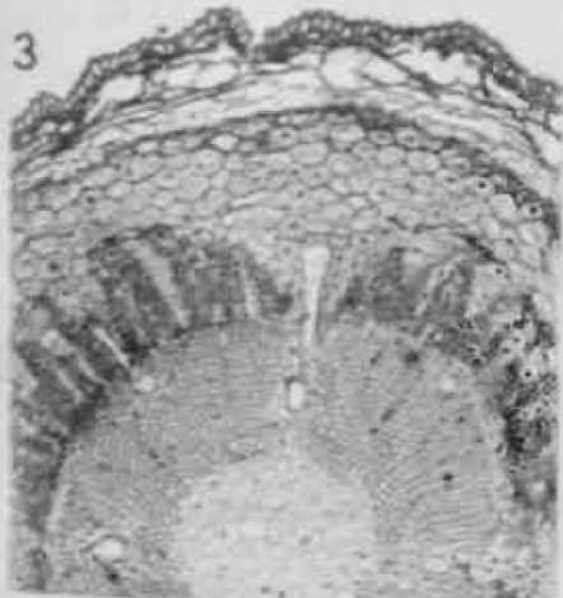
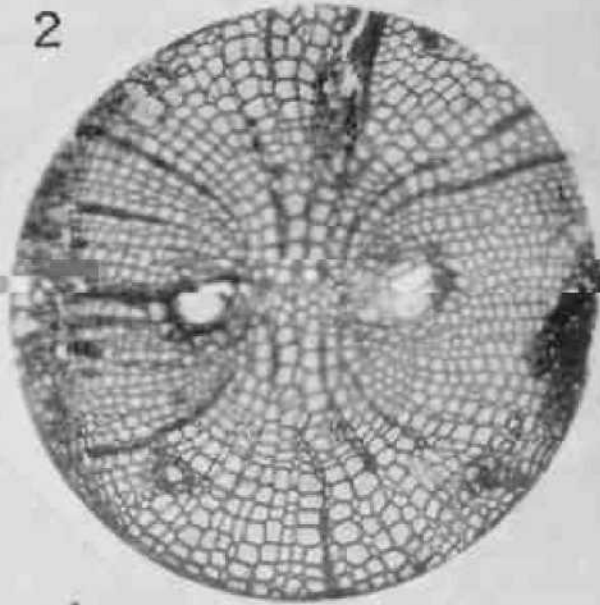
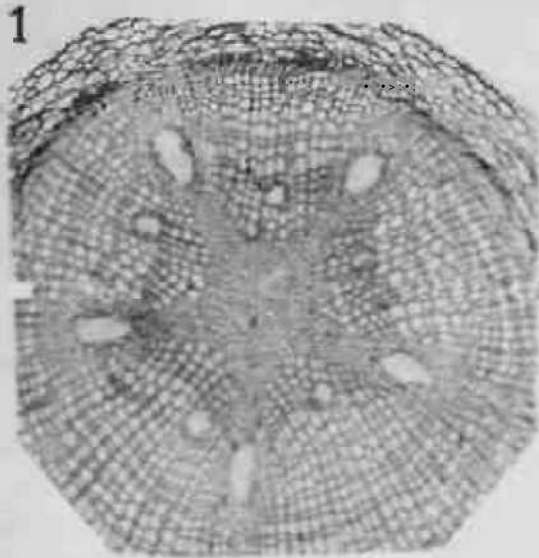
... 14. University of Toronto, Canada, where his work was stored at the University of Toronto. Innumerable kindnesses were shown by Prof. K. E. Murray and Sifton, to whom I am deeply indebted. It was then continued at the Botanical School, Cambridge, after the award of an honorary degree by the Royal Commissioners of the Exhibition of 1884. I am grateful acknowledgment. Prof. A. C. Seward has been very kind and helpful to Mr. Tom Harris and Mr. A. K. Mitia 101

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## EXPLANATION OF PLATE 37.

- Fig. 1. *Pinus Strobus*. Section of primary root showing large root-pole resin canals. (× 50.)  
 Fig. 2. *Pinus resinosa*. Section of lateral root with two root-pole canals, in one of which the lenticel is closed. (× 80.)  
 a. Section of hypocotyl near the cotyledonary node. A horizontal canal ending in a bulb is shown leading from a root-pole canal. (× 80.)  
 Fig. 4. *Pinus excelsa*. Section of hypocotyl. The four root-pole canals are seen near their upper ends. Two canals in the secondary wood are also shown. (× 45.)  
 Fig. 5. *Pinus excelsa*. Section of epicotyl. (× 100.) For description see text, p. 22.



RESIN CANALS IN SETPUNG CONIFEKS.

## HOOKER LECTURE.

THE SWISS NATIONAL PARK.

(With PLATES 38-40.)

THURSDAY, 10TH APRIL, 1926.

BY CARL SCHROETER, F.M.L.S.

With great pleasure I have accepted the invitation to give the Hooker Lecture before the Linnean Society: in the first instance, because I have now the opportunity to thank you personally for the great honour you have bestowed upon me in electing me a Foreign Member of your Society. I am proud to be so closely connected with one of the most renowned biological societies of the world, and will try to show myself worthy of this distinction, which I owe more to the friendly feelings of my British friends than to my scientific merits.

Further, I am specially glad to speak in memory of Sir Joseph Hooker, for whom I have the greatest admiration. I admire him as one of the most successful systematists. That great work, the 'Genera Plantarum,' was possible only in Great Britain, where two men, using the unrivalled Kew Herbarium, were able to master the whole world of flowering plants. I admire him as one of the founders of modern Plant geography by his comprehensive studies on the Flora of New Zealand, Tasmania, and the Antarctic regions. I am sure that he would have taken a great interest in the subject of my lecture, because the studies in National Parks are destined to promote geobotanical problems.

I wish to speak about the biological researches in the Swiss National Park; but allow me to give first a short account of the Genesis, of the Ontogeny, so to speak, of our National Park. It is a part of the movement for the protection of Nature, which in Switzerland is becoming a great influence. Our Civil law permits even expropriation in the interest of natural and historical monuments, and many organisations are at work in this direction. Our numerous ornithological societies provide for the protection of birds in manifold ways; our society of foresters is interested in the conservation of interesting woods: our Liga für Heimatschutz protects the beauties of our landscape against disfigurement, and the Swiss Society of

Naturalists has created a special commission for the Protection of Nature, which has a subcommission in every single state of the Federation. The crown of the building is our "Naturschutzbund," the League for the Protection of Nature, which has now almost thirty thousand members paying an annual contribution of two francs, or fifty francs for life-membership. I would be very glad to be able to take back to Switzerland a long list of British Life-members, for the Conservation of Swiss nature is for the sake of mankind.

Let me sum up the results hitherto reached by these efforts. We have saved about four hundred erratic "blocs" from destruction; several times we have, together with the league for the conservation of scenery, protected mountains against profanation by railways—you will remember the danger menacing the Matterhorn! About fifty species of beautiful trees are reserved. Every canton has now its law for the protection of plants. About fifteen interesting fens and about twenty bird-asylums are being protected. Some asylums for marmots have been created, and the so-called free mountains, where shooting is forbidden, are also a valuable protection.

But the most effective, the most useful, the most durable measure was no doubt the creation of the Swiss National Park, situated in the Lower Engadine. It covers one hundred and forty square kilometres, equal to about fifty-four square miles. It contains the following parts:—

1. The central part—Val Oluozza, Tantermozza, Praspöl, Fuorù, and Stavelchod,—ninety-seven square kilometres, belonging to the parish of Zernez and taken on lease by the Government of Switzerland at a rent of twenty thousand francs; the leasehold is a sort of contract of service for ninety-nine years, which can be revoked only by the Government.

2. The western part—Val Trupchum, Muschauns, and Mela,—ten square kilometres, belonging to the parishes of Campovasto and Scans, taken on lease of ninety-nine years.

3. The eastern part—the left flank of the valley of Scarl with the secondary valleys of Mingèr, Foraz, and Tavru,—thirty-two square kilometres, belonging to the village of Schuls, which would lease only for twenty-five years. As the Government will take a lease only of ninety-nine years, it devolves on the Naturschutzbund to pay the rent of six thousand francs.

4. The intermediate part—Val Niiglia,—twelve and a half kilometres, belonging to the parish of Valcava, and taken on lease by the Government at a rent of eight hundred francs.

The following rules and regulations are in force for the whole region. Human interference is absolutely excluded from the whole region. Shooting, fishing, manuring, grazing, mowing, and wood-cutting are entirely prohibited, no flower or twig may be gathered, no animal killed and no stone removed—even the fallen trees must remain untouched. In this way absolute protection is secured for scenery, plants, and animals: Nature alone

« dominant. Anyone may visit the Park, hut only simple alpine shelter-huts are provided, no hotels being allowed to be erected. Camping and the lighting of fires is prohibited. The custodianship of the Park is entrusted to four resident keepers.

The management of the whole is in the hands of five trustees, nominated by the Government. The State has further pledged itself to contribute a sum not exceeding thirty thousand francs per annum for the rent of the Park\*. The Swiss League for the Protection of Nature is bound to pay the cost of the construction and upkeep of paths and huts, equipment, and salary of the guardians, and scientific research in the Park. Moreover, the Swiss Society for the Advancement of Science is bound to organize these researches.

The district is peculiarly suitable for a National Park, for the following reasons. Its extension in both a horizontal and vertical direction is sufficient to ensure the reconstitution of a natural equilibrium; its mean elevation above sea-level is considerable, so that the snow-line lies as high as 3000 metres and the alpine tree-limit is at 2300 metres. Alpine life, therefore, can be widely developed in the area. In wildness and naturalness, as in loneliness and seclusion, it is scarcely surpassed anywhere in Switzerland. It is very sparsely populated, so that the prohibition of forestry and grazing operations involves but little hardship on its human population. It possesses extensive forests, of which the 2600 hectares of dense forest of erect mountain pine (*Pinus montana* var. *arborea*) deserve special mention. There are also magnificent forests of *Finns Cembra*, mixed woods of spruce and larch (*Picea cembra* and *Larix europcea*), a peculiar mountain race of Scotch fir (*Pinus tylostris* var. *engwintemis*), and extensive areas occupied by the creeping mountain pine (*Pinus montana* var. *prostrata*). In addition to the great abundance of conifers, there is also a rich herbaceous flora, the great variety of geological substrata rendering possible the existence of both calcicole and calcifuge plants. The dividing-line between the floras of the western and eastern Alps passes through the region. In the National Park there is therefore a mingling of eastern and western forms, many eastern species, so far as Switzerland is concerned, appearing only in this district. Animal life, too, is abundant: chamois, marmots, deer, roes, foxes, mountain- and heath-cocks, golden eagle, etc., enlivening the landscape.

Even now, ten years after the beginning of reservation, the favourable effect is clearly visible: the flora of the now abandoned pastures has developed splendidly; we see real gardens of edelweiss, containing plants with fifty capita, and the number of animals has much increased—we counted for instance in 1918 twelve deer, in 1925 ninety. The roe has increased in the same time from sixty to one hundred and ninety, chamois from one thousand to twelve hundred and fifty, mountain-cock from ten to sixty, heath-cock from forty to one hundred and ninety, ptarmigan from one hundred and twenty to three hundred and ten, and golden eagle from fifteen to forty.

Some have criticised us for protecting beasts of prey, such as the fox and eagle; but we must not forget that these animals are exercising a very wholesome hygienic influence, as they kill the sick animals in the first instance! In a certain Bohemian district the foxes had been exterminated, and owing to this an epidemic disease of hares had so increased that foxes had to be introduced. We even hope that the bear, which has disappeared from Switzerland—the last bear was killed in 1904 in Val Minger, in the National Park, -will make his reappearance.

• The splendid alpine animal, also disappeared from Switzerland in 1809, but there still exists a colony in the Italian Alps, in the Valley of Aosta. From this colony young animals have been brought to St. Gallen, where there exists now a flourishing colony. Also in Interlaken a colony of ibex has been established, and from these colonies we are now trying to reintroduce the ibex into our Alps, and up till now we have already four wild colonies, one of which is in the National Park. Its former existence there has been proved by old documents and by a skull found in the National Park.

For science the park represents an invaluable field for observation, unique because of the absolute exclusion of man's interference with the natural equilibrium. All the changes from the primitive state by the secular influence of shooting, fishing, woodcutting, cultivating, pasturing, grazing, haymaking, manuring will have to disappear gradually and the old primitive biocenose will have to be re-established. It is a grandiose experiment to create a wilderness.

It will be the principal task of scientific investigation to study all the successive stages of this return to the primitive stage. Of course, the studies must extend over a very long time. As a basis a complete catalogue of all living beings must be made and an intensive study of the biocenoses.

The successive changes will have to be investigated on a series of typical stations by means of exact analyses of the flora and fauna at long intervals, showing the different stages.

In this way the reclamation of pasture and meadows by the original forest and moorland, also the changes in animal life, the flora of the original condition has been eventually restored, we plants are in the district; also the mode of regeneration of forest in the home be elucidated, the tree-forest which in our country were everywhere by human influence, will reach its

at our park by man or domestic animals makes our Park an invaluable natural laboratory for innumerable observations

on the biological life of plants and animals. A great mass of data, especially about insects, will be gathered by the daily observations of our guardians. Many investigations which otherwise would be subject to disturbance may be safely accomplished: for instance, on fructification when insects are excluded, Parthenogenesis, hybridization, the effect of protection by snow, the longevity of perennial plants. By the work of successive generations of investigators it will be possible to follow up the truly natural successions and changes occurring within the area and to study the relations between soil, climate, and organism.

The Swiss Society for the Advancement of Science has enthusiastically undertaken the task of scientific investigation in the National Park, and in 1917 a special commission of fourteen members was elected. This has formed four sub-commissions: geographico-geological, climatological, botanical, and zoological. Detailed programmes for these investigations have been elaborated and quite an army of collaborators has been appointed, until now no fewer than forty investigators have worked in the Park. Travelling expenses and maintenance are paid by the Naturschutzbund. The results are published in the Annals of the Swiss Society for the Advancement of Science. Up to the present three zoological papers have been published and a botanical one is in print.

What, now, are the principal scientific results hitherto gained? Even before the reservation period the Lower Engadine and the Ofendistrict had been botanically explored. We have a Flora of the Lower Engadine by the late Prof. Braun, a geo-botanical Monograph of the Ofendistrict by Brunnier, a paper on the flora of the National Park by myself, and a very comprehensive report with an excursion in the Lower Engadine and in the National Park by Braun, and many sociological studies. The Lower Engadine belongs to the division of the Central Alpine pine valleys, characterised by a continental climate and many xerothermous plants. An interesting fact is the non-conformity of the immigration paths of the flora with the road of the valley: the most characteristic plants of the Lower Engadine have not come along the Inn, but from the southern valley of the Pintschgau over the pass of the Töschenscheideck.

The complete scientific investigation organised by our commission being still in progress, we can give here only the provisional results as published in the annual reports.

The meteorological subcommission under the presidency of the well-known director of our central meteorological station, Dr. Maurer, has established three stations in the Park, at 1810, 1880, and 1950 metres above sea-level, with thermographs, sunshine recorders, and totalisator. The records show clearly the extreme continental character of the climate. There is a great difference between the extreme temperatures. For instance, the maximum at Buffalo is 23°C, the minimum 33°C.—a difference of 56°C. The sky is quite Italian in its clearness: in 1922 we had 2000 hours of



sunshine—almost as much as in our sunny Tessin, the "sunny verandah of Switzerland." Continental is also the very slight precipitation, 600 to 900 millimetres, our district being among the driest regions of the Swiss Alps.

The geographico-geological subcommission, directed by Prof. Chaix, from Geneva, has studied especially the interesting phenomenon of "block-glaciers, those wandering masses of blocks consisting of the moraines of dead glaciers, buried totally under the moraine shingle. The geological monograph of the district by Spitz and Dyrenfurth will be completed by our geologists.

The botanical subcommission under the direction of Prof. Wilczek, of Lausanne, has occupied thirteen collaborators with the following studies. The over-manured resting-places of cattle with their nitrophile vegetation have been analysed and photographed for the purpose of studying the changes in vegetation with the decrease of manure. Permanent quadrats have been laid in different associations in order to study the slow successions. The associations of plants are studied by the sociological system of Dr. Braun-Blanquet, together with investigations on the soils, hydrogen ion concentration, contents of humus, and amount of calcium carbonate present. A paper now in print by Braun and Jenny on the alpine associations has shown very interesting results regarding the astonishing constancy of hydrogen ion concentration in the Ourvuletum, the association dominated by *Taraxacum officinale*. Also the progressive acidifying of soils has been demonstrated very clearly. The floristic exploration has led to the discovery of numerous new forms of plants—e. g., *Draba ladina* Braun-Blanquet, a new species of a group hitherto purely septentrional, also a xerophytic variety of *Poa alpina* and several new mosses and liverworts.

The study of vertical distribution in connection with the continental climate has furnished many records of altitude—e. g., *Rhododendron gtnium* as high as 2840 m., and seven new plants for the snow region. Also many observations have been made on lichens, fungi, and algae, and the microbes of the soils are studied quantitatively and qualitatively. A great many biological observations have been made, and the vernacular names of the localities have been studied because they often give interesting information about former vegetation. A great many photographs of vegetation and habitats were taken in order to record the present state.

Our zoologists have published three papers: one, treating of the molluscs and referring to sixty-seven snails and mussels, particularly those inhabiting calcareous districts, as the primitive non-calcareous rocks are almost destitute of molluscs. The dryness of the climate seems responsible for the lack of large Hechides. As with plants, the main way of immigration of molluscs runs over the Hechenscheideck, and not along the Inn valley; several species are Mediterranean and three (*Zi...a\* engadinL.*, *Camp^ +\*\** »ad *VeHigo Zsctekkei*, a new species) are endemic. Dr. HofmSinner \*

a paper on Hemiptera, listing one hundred and eighty-one bugs and thirty-six  
 in a e and giving the same results as regards immigration. The Collem-  
 treated by Dr. Handschin, are represented by ninety-five species and  
 and twenty varieties. Thirty species are new to Switzerland and seven species  
 varieties are new to science. The great number of high alpine and  
 forms is surprising: fifty-two species, nil endemic or boreal-alpine.  
 The same author has found about 1400 species of Coleoptera, among these  
 being twenty new species, all coming from the east. The Hymenoptera are  
 also very numerous—for instance, not fewer than 350 species of Icheumonids  
 have been found. Dr. Pictet, of Geneva, well known as a lepidopterist, has  
 found many local races. The paths of immigration are different in this group  
 from the others; they come briefly from the Minister valley and from the  
 south, and Livigno along the valley of the Spöl. Dr. Barbev, a forester  
 and a specialist on noxious insects, has given special attention to the question,  
 whether the falling decayed wood of the National Park, which is not  
 removed, will become a danger to the neighbouring woods as a breeding-  
 place of *Bostrychius*. He denies absolutely that there should be any appre-  
 hension on this score, adding that the primeval forest with its natural  
 equilibrium suffers less from insects than does the cultivated forest. The  
 same is studied by an experienced hunter, who states with pleasure the  
 great number of young chamois.  
 There is a good reason to believe that from the intense activity of our forty  
 investigators we shall get eventually a complete idea of the inorganic and  
 organic nature of our National Park. Three specially favourable conditions  
 are to be mentioned: the absolute exclusion of human interference, the  
 methodical collaboration of many observers, and the possibility of secular  
 observations in this absolutely reserved area.

A trip through the Swiss National Park delights us not only by the  
 wonderful scenery, by the wealth of Flora and Fauna, by the unique  
 opportunity for scientific investigation, but also by the idea that a whole  
 Nation has solemnly taken a vow that here the whole must be preserved for  
 all time, that all personal advantage and all material profit are to be disregarded.  
 A patriotic deed, the educational effect of which is very highly to be esteemed  
 in our materialistic world.

Let me finish with the wish that I shall have at some time the very great  
 pleasure of guiding a large party of members of your Society through our  
 beautiful National Park.

[The lecture was illustrated by over seventy coloured lantern-slides of the  
 scenery, specimen trees, and alpine animals.]



Fig. 1. Linard (8414 m.), the **a** **b** **c** **d** **e** **f** **g** **h** **i** **j** **k** **l** **m** **n** **o** **p** **q** **r** **s** **t** **u** **v** **w** **x** **y** **z** of the Lower Eocene.



Val Minger with Pix Plavna behind (3160 m.).  
The conifers are *Pinus Cembra* and *Pinus montana* var. *prostrata*.



The "fighting zone" (Kampfzone, "zone contestée" of de Candolle) between the limit of the dense  
fir.1 and l.h. timber-line, at Mount Caschera (*Larix europaea* and *Pinus Cembra*).



Forest of erect Mountain Pine (*Pinus montana* var. *arabica*).

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## ERRATA.

- P**
- 63, line 23, for (O. F. Muell.) Schrank read (Schrank), u. <sup>66</sup> Muell.
- » » 23, for Bacillari® read Bacillariese.
- 95, ,, 35, for *Perdinium* read *Peridinium*.
- 115, ,, 9, for *Psychophyton* read *Psychrophyton*.
- 123, ,, 28, for *Amrrica* read *America*.
- 134, ,, 10, for 2T. frj^om read *C. trijlera*.
- 180, ,, 16 from bottom, /or d<5veloppent read de\*veloppemeni,
- 225, ,, I, for *G. brachiatum* read *C. hrachiatum*.
- 258, ,, 2 from bottom, for *Vernonw\** read *Vernonieffl*.
- 281, ,, 3, for *mirocephalum* read *micrtwephalum*.
- 281, ,, 16, for broa rearf broad.
- <sup>42</sup>7. » 7, /or 1923 read 1922.
- 428, ,, 4, for aud read and.
- 428, ,, 2 from bottom, /or This read A.
- 431, ,, 24, for nt rend ut.
- 442, ,, 3 from bottom, for *Gaditantf* read *gaditana*.
- 455f 9i 2, /or minor rearf minores.
- 461, ,) 14, actf, after d'Alger: No. 184.
- 462, ,, CO, for corolla read corollâ.
- 465, ,, 11, for deacriptien read description.
- <sup>4a</sup>t ii <sup>4</sup>> <sup>pr</sup> officinalis *Pugs. riad* officinalis *Linn.*
- \*&, ,, 27, for *Caroliana Pugs,* read *Caroliana Pugs.\**
- 485, ,, 10 from bottom, for *Unibelliflor»* read. ~~Unbelliferae~~.
- 512, ,, 22, for The artistf read The botanist.
- 519, ,, 11, for *hemaphrodita* read *hermaphrodita*.

# NOTICES.

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