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XIX.—Contributions towards a Knowledge of the Anatomy of the Lower Dicotyledons. II. The Anatomy of the Stem of the Berberidaceæ. By R. J. HARVEY-GIBSON, C.B.E., D.L., M.A., Professor of Botany, University of Liverpool; and Elsie Horsman, M.Sc. (With One Plate.)

(MS. received November 22, 1918. Read January 20, 1919. Issued separately May 21, 1919.)

#### INTRODUCTORY.

The present paper is the second of a series of investigations into the anatomy of the lower Dicotyledons (1), aiming at the accumulation of anatomical data which, it is hoped, may prove of service in elucidating the phylogeny of the complex of orders usually regarded as situated somewhere near the base of the Angiosperm phylum. The continuance of the War has again materially retarded these investigations, and has also rendered it almost impossible to obtain material from abroad that would, doubtless, have been available in peace time. We are greatly indebted for substantial assistance in this relation more especially to Sir David Prain, F.R.S., Director of the Royal Botanic Gardens, Kew, and to Sir Frederick Moore, F.R.S., Director of the Glasnevin Gardens, Dublin, and to them we tender our grateful thanks.

According to PRANTL (2), the order Berberidaceæ includes eight genera—Podophyllum, Jeffersonia, Diphyllia, Achlys, Nandina, Epimedium, Leontice, and Berberis (including Mahonia). To these LORSY (3) adds Hydrastis and Glaucidium, which PRANTL places among the Ranunculaceæ. The Lardizabalaceæ are included in the Berberidaceæ by SOLEREDER (4), as also by BENTHAM and HOOKER (5), while Berberidopsis, sometimes placed in Berberidaceæ, is included in Flacourtiaceæ by other authors. In the following pages seven of the eight genera of Berberidaceæ, as enumerated by PRANTL, and representatives of four genera of the Lardizabalaceæ, viz. Lardizabala, Stauntonia, Akebia, and Decaisnea are discussed.

For detailed treatment the common Barberry, *Berberis vulgaris*, L., has been selected, and its anatomy is compared with that of several other species of the genus. This has provided a basis on which to found a discussion of the other genera referred to, and has suggested certain general remarks on the relationships of the various types dealt with, both to each other and to members of other orders.

#### THE ANATOMY OF THE STEM OF BERBERIS.

*Berberis vulgaris* is a shrub with small simple leaves, with solitary spines formed by prolongation of the mid-ribs. Occasionally two additional spines are

developed as marginal outgrowths towards the apex of each leaf. The flowers are yellow and trimerous, suggesting an affinity with Monocotyledons.

The most prominent feature shown in a transverse section of the stem is the deeply-seated ring of cork cells with remarkably large lumina. The tissues are arranged in the following sequence (figs. 1, 2):—

1. An epidermis of regular rectangular cells with cuticle and numerous stomata.

2. One or two layers of thin-walled cells with intercellular spaces. In older stems these cells persist in that condition, but in other cases they are crushed by the growth of tissues more centrally placed.

3. These cells are bounded internally by a ring of sclerotic tissue three or four layers thick. In very young stems this ring is not quite continuous, but is interrupted by thin-walled cells, usually in the interfascicular regions, agreeing in this respect with the similar ring found in the Papaveraceæ (1). In older stems the sclerotic ring increases considerably in thickness and complete continuity is established, though later it is again segmented into patches as a result of the tension set up by the growth of the internal tissues and as a preliminary to being cast off by the cork.

The individual fibres are long, and their endings are either truncate, oblique, or tapering. They all show simple pits. Occasionally this tissue, by hypertrophy, produces ridges, although other species show this to a much greater extent than *B. vulgaris*. SOLEREDER considers this ring as belonging to the outer pericycle.

4. Immediately within this sclerotic band is the deeply-seated cork, which at first consists of one layer of regular, large, thin-walled cells with remarkably wide lumina. These cells are two, three, or more layers deep in older stems.

5. Next follows a region of cortical cells, the outer being small and compact, the inner larger and having intercellular spaces. All are thin-walled and have protoplasmic contents. In the medullary ray region, "berberin" is present in the form of yellowish-green granules, and often the whole cell contents are impregnated with it; some cells in this region contain also klinorhombic crystals of calcium oxalate, which almost completely fill the cell lumina (fig. 3). Berberin is an isoquinoline alkaloid, insoluble in water, and hence can be best seen in sections of fresh material mounted in water. Spirit in which Berberis material has been preserved becomes yellowish-brown owing to the dissolved "berberin," which remains as a resinous deposit on evaporation. Further research is at present being carried out on the chemical composition and reactions of this substance.

According to SOLEREDER, the fibrous ring, the cork, and the cortical region just mentioned form a composite pericycle.

No endodermis is differentiated, for ordinary cells of the cortex abut directly on the vascular bundles.

In the young stem the vascular bundles are distinct, the interfascicular regions

being composed of sclerotic tissue; but later the bundles, together with the broad primary medullary rays, form a complete ring of lignified tissue (fig. 1).

The phloem consists of very small elements arranged in radial rows. In older stems it shows sieve tubes with bevelled ends occupied by sieve plates and callus, with slime strings across the plugs from segment to segment; but no grouping of sieve plates into areas is observable. This may be due to the very small size of the sieve tubes, which also prevents the definite location of plates on the lateral walls, though they appear to be present. Some of the sieve tubes are accompanied by companion cells, although this is by no means an invariable rule. Phloem parenchyma is abundant, and the cells show intercellular communications. Lignified fibres with deep simple pits are also present. They are short and spindle-shaped, and in cross section show strongly thickened walls and small lumina, thus differing from the pericycle fibres, which are much wider and have walls less strongly lignified. These bast fibres are formed in tangential rows in the inner secondary phloem and border the lamellæ into which the phloem is divided as growth proceeds, thus recalling the alternating bands of *Vitis*, though they are developed to a much less extent. A few scattered fibres are also found in the outer primary phloem, but no stone cells are present.

Crystals and "berberin" granules are found in the medullary ray region of the bast, as above mentioned. The bast fibres are not continued across these regions.

In the early stages the xylem elements are regular and similar in size and shape, with wide lumina, some showing remains of protoplasmic contents. Later the lignification becomes more pronounced, the lumina decrease, and the arrangement in radial rows becomes more obvious. Comparatively large polygonal vessels are distinguishable in the protoxylem and in groups towards the centre of each vascular bundle. In the protoxylem the first formed vessels are spirally thickened, the innermost spirals being right-handed and later ones left-handed, as pointed out by DE BARY (6). The other vessels possess bordered pits with slit-like apertures (fig. 5), the slits lying at right angles to the axis of the vessel; many have faint spiral thickenings in addition to pits, similar to those recorded for *Romneya* (*Papaveraceæ*) (1) and for *Dendromecon* by LÉGER (7). Most of the xylem consists of prosenchymatous fibres with simple pits on all their walls and often containing starch, particularly in the winter condition. These fibres always occupy the regions abutting on the medullary rays. SANIO (8) says that septate fibrous cells are found only in the first annual ring. This does not seem to be invariably true, although the septa are not so frequent in the fibres of the second and subsequent years. Comparatively few tracheids are present, and these have bordered pits accompanied by spiral thickenings, as in *Taxus*. There seems to be little difference between the pitted fibres and the pitted tracheids. Spiral tracheids resembling fibres are also present.

The predominance of stereome and the reduction in the number of conductive elements is to be correlated with the xerophytic character of the plant. The small amount of leaf surface, and the consequent reduction in transpiration, the necessity for protecting the cell contents from the intense insolation to which *Berberis* is subjected in its native habitats (Asia, South and Central America), may also be associated with the predominance of sclerosis and the large development of wood fibres.

Broad primary medullary rays persist, and consist of markedly sclerotic cells which, in transverse section, closely resemble the xylem elements, but are often larger than the adjacent xylem fibres. The rays are three or four cells wide, and the cells have rounded ends. They are elongated radially, the radial diameter being in many cases almost twice the tangential one. All the walls show numerous simple pits, and most of the cells are well filled with starch grains during the winter. No secondary rays are produced. The contents of the medullary ray regions of the cortex have been previously described.

The medulla is heterogeneous; the cells near the protoxylems are smaller than the rest and have well-thickened walls. They show nuclei when young, and starch grains in the winter condition at all ages. Numerous simple pits occur on all their walls. The central cells are larger and become polygonal by mutual pressure; they are thin-walled and devoid of contents.

The petioles are slender and wiry. In the main portion of the petiole there are four vascular bundles surrounded by sclerenchyma, but these unite as the lamina is approached. In the basal region there are only three vascular bundles, which later on divide into four. As the petiole expands into the lamina the vascular bundles again rearrange themselves into three bundles.

#### *Other Species of Berberis.*

Most of the species of *Berberis* exhibit features similar to those described for *Berberis vulgaris*, among which the following structural variations may be noted. Spines occur on the stems of some species. They are outgrowths from single epidermal cells, and are present in *B. Yunnanensis*, Franch., *B. stenophylla* × hort., *B. angulosa*, Wall., *B. Wallichiana*, DC., *B. empetrifolia*, Lam., and *B. Darwinii*, Hook. (fig. 6). In the last-mentioned species they are much longer, are curved, and have transverse partitions.

The sub-epidermal parenchyma in *B. aristata*, DC., *B. stenophylla* × hort., *B. empetrifolia*, Lam., and *B. aquifolium*, Pursh., shows foldings in the cell walls as described for *Corydalis racemosa* (1), but in the present instances the folding appears to be caused by the pressure of internal tissues acting in opposition to the resistance offered by the epidermis. In the older stems the compression increases until these cells are cast off along with the other tissues external to the deeply-seated cork.

The sclerotic pericycle in some cases is increased so much as to form ridges in the stem, e.g. in *B. angulosa*, Wall. (fig. 8), and *B. Yunnanensis*, Franch.

The spines so characteristic of the Berberidaceæ consist mainly of sclerenchymatous fibres and are obviously modified leaves, as shown by their position at the nodes and by their structure. The sheath of sclerenchyma almost entirely encloses two cavities filled with loosely arranged thin-walled cells and one or more vascular bundles (fig. 9). Stomata are found only on the incurved surface, where they are abundant. The sclerotic fibres are continuous throughout the spine to the tip, which is formed solely of fibres covered by epidermis.

The inner layers of the heterogeneous pericycle, which consist of thin-walled parenchyma, are often so loosely arranged as to produce conspicuous cavities crossed by cellular bridges (fig. 10). In some species these layers are increased locally, contributing to the production of the stem ridges.

Resin ducts are present in the phloem in some cases. In transverse section they appear to consist of single large cells with lignified walls showing oval pits (fig. 11).

In the young stem of *B. Jamesoni*, Lindl., vessels and tracheids with comparatively large lumina predominate, but as the stem increases in age and girth lignified fibres are developed bordering the medullary rays, as in *B. vulgaris*.

According to HABERLANDT (11), "medullary rays always abut directly against xylem parenchyma on their flanks as well as on their upper and lower borders." This suggests that the prosenchymatous fibres which always border the medullary rays may be parenchyma cells modified to give additional support to the stem (fig. 12). They are well supplied with simple pits, while some show septa and many contain starch grains.

Several species show oval bordered pits longer than those of *B. vulgaris*, e.g. *B. Sieboldii*, Miq. Others show bordered pits in conjunction with faint reticulate markings, e.g. *B. Wallichiana*, DC., and *B. Yunnanensis*, Franch. The former also shows loose reticulate markings in vessels without pits.

A few species show a slight development of normal xylem parenchyma, e.g. *B. stenophylla* × hort., *B. Jamesoni*, Lindl., *B. Sieboldii*, Miq. The parenchyma when present always surrounds the larger vessels in the protoxylem regions, and is usually lignified and similar to the xylem fibres in transverse section.

In *B. angulosa*, Wall., the greater portion of the wood consists of tracheids with round bordered pits resembling those of *Pinus*, but smaller in size.

SOLEREDER states that scalariform markings occur occasionally in *Berberis*; no such thickenings were found in any of the species of *Berberis* examined, though they are to be found in *Podophyllum* and *Diphylleia*.

There is very little variation in the medullary rays; most of them closely resemble those of *B. vulgaris*. The ray cells are well lignified, thus rendering them hardly distinguishable from the surrounding xylem. They vary in width from two to eight cells, the widest being found in *B. Wallichiana*, DC., where they have

very abrupt endings. In the very few cases where secondary rays have been found, they are by no means uniform in their occurrence, a transverse section showing perhaps only three or four secondary rays to a large number of primary ones. The presence of secondary rays is always associated with wide bundles and narrow primary rays.

The pith in the majority of cases is heterogeneous, as in *B. vulgaris*, L. Many species show solitary klinorhombic crystals of calcium oxalate in addition to starch in the peripheral cells, e.g. *B. aquifolium*, Pursh., *B. stenophylla* × hort., *B. Jamesoni*, Lindl., *B. empetrifolia*, Lam., *B. Darwinii*, Hook.

Some species show a pith sclerotic throughout, but here also the central cells are often larger than the peripheral ones, e.g. *B. Darwinii*, *B. angulosa*.

The general plan of structure of the stem in *Berberis* (*Mahonia*) *aquifolium*, Pursh., is the same as that of other species; a sclerotic pericycle and cork cells with wide lumina are present; the xylem shows the same predominance of lignified fibres and the same broad primary medullary rays. The bordered pits have round apertures, as in *B. angulosa*, in contrast to the slit-like pits most frequent in the genus. No lignified fibres occur in the bast. The pith is sclerotic throughout.

#### SUMMARY OF ANATOMICAL CHARACTERS OF BERBERIS.

1. There is a continuous sclerotic ring of pericycle fibres, similar to that present in the Flacourtiaceæ.

2. Cork cells with remarkably wide lumina occur, as in some Menispermaceæ.

3. Bast fibres occur in tangential rows in the secondary phloem, agreeing in form and arrangement with those of Lauraceæ and some Magnoliaceæ.

4. The xylem is composed chiefly of strongly lignified fibres with occasional thin transverse septa, as in Lauraceæ and Flacourtiaceæ.

5. The largest vessels and some of the tracheids exhibit bordered pits with slit-like apertures, while most species show a combination of bordered pits and spiral thickenings.

6. Very little parenchyma occurs in the xylem, in which particular it again agrees with that of the Menispermaceæ.

7. Broad lignified primary medullary rays are characteristic of the genus, with only very occasional secondary rays. In the Menispermaceæ the rays are similar in all respects, save that some cells in the broad rays may not be lignified.

8. The pith is usually heterogeneous, though in some species the cells are sclerotic throughout. Heterogeneous pith also occurs in Magnoliaceæ, some Lauraceæ, and Menispermaceæ.

9. The phloem consists of sieve tubes, companion cells, phloem parenchyma, and bast fibres; the two former occur principally in the primary phloem, while the secondary phloem consists mainly of parenchyma and bast fibres.

10. Spines occur both as epidermal outgrowths from the stem and as modified leaves.

The Epimedæ include *Epimedium*, *Vancouveria*, and *Nandina*, and doubtfully also *Jeffersonia* and *Achlys*. With the exception of *Nandina*, none of the genera investigated are woody.

*Nandina domestica*, Thunb., is a Japanese shrub. In the young stem there are distinct ridges formed by the development of sclerenchyma, especially in the neighbourhood of the vascular bundles. The vascular bundles are well separated by small cells which afterwards form medullary rays, 5-8 cells in width, in the older stages. The ridges gradually disappear owing to the development of sclerenchyma levelling up the depressions. The four or five large vascular bundles have rather smaller ones alternating with them, but all traces of this distinction disappear in older stems.

When in the young state the phloem areas are distinctly rounded in section and are destitute of lignified fibres. The xylem consists mainly of vessels with wide lumina, together with a few parenchymatous cells, while simple pitted fibres border the medullary rays, as in *Berberis*. The vessels show a variety of markings: spiral in the protoxylem, in other parts reticulate; slit-like pits merging into reticulate and bordered pits with slit-like apertures. Occasionally tracheids with bordered pits are also present.

When young most of the pith consists of thin-walled cells, but later it becomes entirely sclerotic. The pith is relatively large, comprising about 80 per cent. of the area in the transverse section of an old stem. Some of the cells are elongated and show simple pits; they appear to act as storage organs. Some near the periphery show peculiar forked endings.

*Vancouveria hexandra*, C. Morr. and Dec.—The species possesses an underground stem or rhizome in addition to the normal aerial stem.

The aerial region in the young state has a slightly cutinised epidermis followed by two or three rows of cells which are elongated longitudinally and show no intercellular spaces. Next follow three or four rows of small sclerotic fibrous cells forming a distinct ring, but merging into larger thin-walled cortical parenchyma, as a rule devoid of contents. Through this tissue run widely separated vascular bundles. In the young condition more than half of the bundle is composed of phloem without fibres. The xylem consists entirely of spiral and pitted vessels with comparatively wide lumina, while the protoxylem is flanked by small sclerotic cells in older stems.

The xylem of the vascular bundles in the rhizomic region is so embedded in sclerotic tissue that together they form a complete ring of stereome, except in some old specimens where the continuity is interrupted and the internal and external parenchymatous areas are united by broad bands of non-sclerotic tissue. The phloem occurs in patches outside the stereome ring, and consists mainly of sieve tubes and companion cells. The sieve plates are in some cases transverse, in others

oblique, while some show sieve plates on their external walls. No lignified fibres occur. The vessels occupying the centre of the bundles show various forms of lignification—spiral, reticulate, or bordered slits. On the lateral borders of these groups of vessels are thickened prosenchymatous fibres which occupy the whole of the interfascicular regions, thus completing the ring of mechanical tissue.

Outside the phloem areas are occasional sclerotic cells among the ordinary cortical cells, and beyond these lies a ring of slightly thickened cells corresponding to the sclerotic ring in the aerial stem. The rhizome thus contains two concentric rings of mechanical tissue—an inner one consisting of the xylem of the vascular bundles and sclerotic fibres, and an outer of sclerotic tissue only. The epidermal cells are thin-walled, and the sub-epidermal tissue consists of fairly large and irregular cells, many of which contain a brown deposit.

All the material examined was herbaceous and showed no signs of any development of cork.

*Epimedium alpinum*, L., shows a structure very similar to that of *Vancouveria*, but some of the vascular bundles are more peripheral, so that their phloems are embedded in the peripheral sclerotic ring. The medulla is markedly fistular. Many of the cortical cells are elongated with large oval pits in their walls, and hence are probably conductive.

In the rhizome the ring of mechanical tissue is incomplete, the bundles being separated by broad plates of parenchyma. In the aerial stem there are two rings of vascular bundles.

*Epimedium sagittatum* agrees with *Vancouveria* so far as the structure of the aerial stem is concerned.

*Jeffersonia dubia*, Benth. and Hook., and *Jeffersonia binata*, Bart., agree with the three previous genera in having their vascular bundles arranged in a ring, some of them partially embedded in the ring of sclerenchyma; in the structure of the xylem—having vessels with bordered slit-like pits, in having a lactunar cortex, and in having a phloem very rounded in section. In *Jeffersonia dubia* the sieve tubes are well developed, with well-marked callus plugs and faint canals across the callus, and the nodes on the median lamella. SOLEREDER says the arrangement of bundles in *Jeffersonia* is Monocotyledonous; but, apart from the fact that some bundles are smaller and rather nearer the periphery than others, the material we have examined presents no evidence in support of this statement.

The chief characters of stem anatomy of *Epimedeæ* may be summarised as follows:—

1. There is a continuous ring of sclerenchyma, pericyclic in origin.
2. The phloem bundles are very rounded in outline and have no fibres. The sieve tubes are larger than in *Berberis*, and in many cases show sieve plates on the lateral walls.
3. The xylem consists chiefly of vessels with fairly wide lumina. Those of the

protoxylem are spirally thickened, the others have reticulate or bordered slit-like apertures.

4. Prosenchymatous fibres occur only in *Nandina* and in the rhizome of *Vancouveria*; in the other genera xylem parenchyma replaces fibres.

5. Except in *Nandina* and in the rhizome of *Vancouveria* the bundles remain isolated, and the interfascicular tissue is unligified.

6. The central parenchyma in *Nandina* becomes sclerotic, but in *Vancouveria* and *Epimedium* only the cells in close proximity to the protoxylem show sclerosis. In all save *Nandina* the cortex tends to become lacunar.

7. The vascular bundles are arranged in a ring, although developmentally constructed from two rings interlocking.

*Achlys triphylla*, DC.—In the aerial stem the bundles are irregularly arranged (fig. 13), and only a few are in contact with the ring of sclerotic tissue, which is similar in position to that in *Vancouveria*, *Epimedium*, and *Jeffersonia*. The smallest bundles are toward the periphery and the largest ones toward the centre, but no definite arrangement in rings is observable. The general appearance recalls the arrangement in *Podophyllum* rather than that in the *Epimedææ*.

The xylem consists chiefly of spiral vessels without fibrous elements. The phloem is rounded in section and consists of sieve tubes with occasional companion cells. The sieve tubes show sieve areas on their lateral walls.

The bundles in the rhizome are arranged in two rings, as noted by TISCHLER (9). The main bundles form an inner ring, while the others, which consist chiefly of sclerenchyma, alternate with them and are nearer the periphery. The cork cells resemble those of *Berberis*; they have wide lumina, are deep-seated and of pericyclic origin. The xylem contains pitted vessels and tracheids. Pericyclic fibres do not occur in the rhizome.

The *Podophylleæ* include *Podophyllum* and *Diphylleia*, and also, according to LOTSY, *Jeffersonia*, *Achlys*, *Hydrastis*, and *Glaucidium*, although the two latter genera are placed by most systematists in the *Ranunculaceæ*. *Podophyllum Emodi*, Wall., very closely resemble *P. peltatum* in anatomical structure, as described by HOLM (10).

Stems of different ages show irregularly arranged bundles, widely separated from each other, the largest being central (fig. 14). With the exception of the cambium present in each bundle, the stem in section has the appearance of a normal *Monocotyledon*.

In the bud stage no sclerosis is present in the cells surrounding the bundles, but later a crescentic mass of sclerenchyma arises on the phloem side. Towards the periphery there is a ring of sclerenchyma in which the phloem of the outer bundles is embedded, as in *Epimedium* and *Jeffersonia*.

At first only a few of the xylem elements are lignified and show spiral markings, later formed units show annular and reticulate thickenings. Xylem parenchyma occurs but no fibres. The phloem appears to consist solely of sieve tubes with

lateral plates and companion cells; as in *P. peltatum*, no fibres and no parenchyma are present.

The material examined was herbaceous and no cork was noticeable, although it is given by SOLEREDER as sub-epidermal in origin.

The rhizome shows a distinct ring of large bundles, with a few smaller ones outside in the cortex, but the arrangement is not as definite as in *Achlys*. There is no peripheral ring of pericyclic fibres such as is shown by the rhizome. In the main bundles the xylem consists of a few scalariform tracheids, wide vessels showing a variety of markings—spiral, loosely reticulate, long oval pits, and bordered slits,—and many parenchyma cells showing no lignification. The phloem is very little differentiated and consists of radially arranged elements, a few of which are sieve tubes, while most seem to be parenchymatous in their nature. The tissue bordering on both phloem and protoxylem consists of smaller cells which are slightly sclerotic, with simple pits in their walls. The central parenchyma cells, which are slightly elongated, contain resin.

The petiole resembles the aerial stem in having a ring of bundles towards the periphery and irregularly scattered bundles in the centre, formed from the bundles nearest the upper surface of the leaf.

*Diphylleia cymosa*, Michx., is very similar to *Podophyllum* in anatomical structure. In the aerial region there is the same ring of sclerenchyma towards the periphery and a ring of bundles with their phloems partly embedded in the sclerenchyma. The other vascular bundles are scattered irregularly, as in *Podophyllum*, and have sclerenchyma on the outer margins of their phloems. The phloem and xylem elements, as also the anatomy of the rhizome and petiole, agree with the description given for *Podophyllum*.

The chief characteristics of the stem of the *Podophylleæ* :—

1. The bundles are scattered, the larger being towards the centre, as in *Monocotyledonous* stems, while the outer and smaller bundles have their phloems embedded in a sclerotic ring.
2. In the aerial axes the main bundles are in the form of a ring with smaller ones more peripherally placed.
3. The xylem consists chiefly of vessels with annular, reticulate, and scalariform thickenings and long, oval bordered pits.
4. No prosenchymatous fibres were found, but unlignified parenchyma cells are present among the vessels.
5. The central parenchyma is practically homogeneous, although a few cells near the protoxylems are slightly sclerotic.

In comparing the stem anatomy of the *Berberideæ*, *Epimedææ*, and *Podophylleæ* it may be noted—

1. That all three subdivisions are characterised by possessing a ring of pericyclic sclerotic fibres in their aerial stems.

2. That the remarkably wide-lumined cork cells which arise on the inner border of the composite pericycle are present in Berberideæ and in the aerial stems of some of the Podophylleæ, but are absent in the Epimedæ and in the aerial stems of Podophylleæ, where the cork is normal in form and sub-epidermal in origin.

3. That in the aerial axes of Podophylleæ the bundles show a "scattered" arrangement, as in Monocotyledons, but that in the subterranean regions the chief bundles form a definite ring, while others are scattered in the cortex. In Epimedæ they are arranged in a ring which appears to be formed by the interlocking of two rings of bundles. In Berberideæ the bundles exhibit the normal Dicotyledonous arrangement.

4. That bast fibres are present in tangential rows in the secondary pith of Berberideæ, but are absent from the Epimedæ and Podophylleæ.

5. That the rigid texture of the Berberideæ is produced by the relatively large amount of prosenchymatous fibres, not present in herbaceous Epimedæ (though in the rhizomes of *Nandina* and *Vancouveria*), nor in the Podophylleæ; while unligified parenchyma is present among the vessels of Epimedæ and Podophylleæ, but not of Berberideæ.

6. That the vessels in all three groups possess bordered pits with slit-like apertures, their greatest diameter being always at right angles to the axis of the vessel. In the Berberideæ these are often accompanied by spiral or reticulate thickenings, but this combination does not occur in the Podophylleæ and Epimedæ.

7. That broad primary medullary rays consisting of lignified cells link up the xylem of the vascular bundles into a complete stereome ring in some, whilst in others (except *Nandina* and *Vancouveria* rhizomes) the bundles are widely separated by undifferentiated parenchymatous cells.

8. That the central parenchyma is similar in all three groups, being composed usually of central thin-walled cells, with thick-walled cells towards the protoxylems. In both Berberideæ and Epimedæ some species show uniformly sclerotic parenchyma. The Berberideæ alone show crystals in the central parenchyma.

9. That the sieve tubes in all genera have sieve plates on their bevelled ends, and occasionally on the lateral walls as well.

10. That the endodermis is not well marked, and that stone cells are conspicuously absent.

In stem anatomy *Hydrastis canadensis* does not resemble Podophyllum, for the vascular bundles are not scattered and the ring of sclerotic pericycle, which is invariably present in all the Berberidaceæ examined, is entirely absent. The anatomical characters suggest that this species is not closely allied to the Berberidaceæ.

The *Lardizabalaceæ* are regarded as a tribe of Berberidaceæ by BENTHAM and HOOKER. They are included in that order also by SOLEREDER, but separated from it by ENGLER and PRANTL and by LOTSY. This order comprises *Lardizabala*, *Stauntonia*, *Akebia*, *Decaisnea*, *Holboëllia*, *Parvatia*, and *Boquila*.

Stems of the following have been examined, viz :—*Lardizabala biternata*, Ruiz and Pav., *Hobbaëlia latifolia*, Wall., *Akebia quinata*, Dec., and *Decaisnea Fargesii*, Franch. They all show marked differences from the Berberidaceæ, but many of these differences may be accounted for by their climbing habits. For instance, vessels of the xylem are much more numerous and have considerably larger lumina than any Berberidaceæ, while prosenchymatous fibres are very few, being replaced by xylem parenchyma which is often lignified and shows bordered pits with slit-like apertures. Thus the supporting tissue which predominates in woody Berberidaceæ is replaced in the Lardizabalaceæ by conductive elements. In common with many other climbers these plants show large sieve tubes. In *Decaisnea* the sieve plates occur on the bevelled ends, the polygonal sieve areas being separated by bands of cellulose, while sieve fields also occur on the lateral walls. Phloem fibres are absent, but on the external margins of the phloem areas are semi-lunar bands of sclerenchyma with very thick walls and packed with calcium oxalate crystals; they appear to be of pericyclic origin and correspond to the ring in Berberidaceæ. The ring in this case, however, is much more irregular since the sclerenchyma is formed in depressions in the interfascicular regions, producing the ridged appearance so characteristic of lianes.

The cork arises sub-epidermally and is normal in character.

*Akebia* shows a well-marked endodermis, the cells being thickened on three sides and thin-walled on the inner, which abuts on the parenchyma.

In many respects the Lardizabalaceæ appear to form a link between the Berberidaceæ and the Menispermaceæ.

The Lardizabalaceæ and Menispermaceæ consist chiefly of climbing shrubs, whilst the Berberidaceæ are not climbers.

1. The cork in Lardizabalaceæ is sub-epidermal in origin, as also in some Berberidaceæ and Menispermaceæ.

2. The pericyclic sclerenchyma occurs in arcs outside the phloem bundles, and since the bundles are close together, the arcs of sclerenchyma unite more or less into a ring. In this respect the Lardizabalaceæ differ from the Berberidaceæ, where the ring is continuous, and resemble the Menispermaceæ, which do not possess a continuous ring but have sclerotic arcs round the vascular bundles connected by groups of stone cells.

3. Bast fibres are absent from the phloem of Lardizabalaceæ and Menispermaceæ, but present in woody Berberidaceæ.

4. The xylem of Menispermaceæ consists chiefly of vessels with large lumina, and this is true also of Lardizabalaceæ, whilst in Berberidaceæ prosenchymatous fibres predominate.

5. All three orders agree in having broad primary medullary rays. In all the non-herbaceous species of Berberidaceæ the medullary ray cells are well lignified. In some species of Lardizabalaceæ all the cells are strongly lignified, but in others

the cells in the centre of the rays are thin-walled, flanked by sclerotic cells. The Menispermaceæ agree with the Lardizabalaceæ in often having unligified medullary rays.

*Berberidopsis*.—HALLIER describes *Berberidopsis* as a syncarpous *Berberis* with points in common with the Flacourtiaceæ, while ENGLER and PRANTL and BENTHAM and HOOKER place it definitely in the Flacourtiaceæ.

An examination of the stem structure of *Berberidopsis corallina*, Hook., presents the following characters (fig. 15):—

1. A thick cuticle is present on the epidermal cells.
2. The external cortex often contains stellate crystals of calcium oxalate.
3. The ring of sclerenchyma is very open and is interrupted in older stems. The cells are short and rectangular and have numerous simple pits in their thick walls (figs. 16, 17). These sclereides correspond to the stone cells in the cortex of young twigs of *Acer* and *Æsculus*, but in these two genera the sclereides accompany sclerenchymatous fibres, the latter being much more numerous, whereas in *Berberidopsis* the sclereides predominate and very few fibres occur. HABERLANDT (11) suggests that these sclereides are cortical parenchyma cells which have penetrated gaps produced in the mechanical cylinder of bast fibres as a result of tensions set up by the growth in thickness of the twigs. The cortical parenchyma cells afterwards become thick-walled and so restore the unity of the now composite mechanical cylinder. The varied shape and arrangement of the sclereides seem to support this view.

4. The cork arises sub-epidermally and is normal in character, the cells being rectangular.

5. The xylem contrasts markedly with that of *Berberis*, the elements are larger, and the main portion consists of large vessels which are slightly thickened and have very loose reticulations forming large irregular pits (fig. 18). Tracheids are present with oval bordered pits.

6. Most of the cortical cells are thin-walled, but a few near the protoxylems are sclerotic, and all of them show simple pits. The more peripheral cells often contain starch grains or crystals of calcium oxalate.

7. No bast fibres are present in the phloem. The information available as to the anatomy of the Flacourtiaceæ is at present very meagre, so that a detailed comparison with the *Berberidaceæ* is not possible. The following points of resemblance may, however, be noted:—

1. In the Flacourtiaceæ the sclerotic ring may be continuous, or in patches joined by bridges or broken up completely into islands.

2. In both the xylem shows wide reticulate thickenings.

3. The medullary rays are numerous and vary from one to four cells in width in both families, but in *Berberidaceæ* the rays are wider and less numerous.

## SUMMARY OF THE ANATOMICAL CHARACTERS OF THE BERBERIDACEÆ.

1. Scattered vascular bundles occur in the aerial stems of the Podophyllæ, the largest bundles being centrally placed. Save that cambium is present, the vascular anatomy closely resembles that seen in Monocotyledonous stems.

2. Bordered pits occur very frequently in the secondary wood, both in vessels and tracheids; the apertures vary in shape, some being circular, others more or less oval with slit-like apertures. Where circular bordered pits occur in tracheids they closely resemble those of *Pinus*, although both tracheids and pits are smaller than in the Coniferæ.

3. The combination of a double spiral thickening and bordered pits is of common occurrence in the woody species of the order; while bordered pits combined with reticulate thickenings occur in some (conf. *Taxus*).

4. The xylem parenchyma is as a rule unligified. Some species show a few lignified cells among the vessels of the protoxylem, but in none are there continuous plates or areas of lignified parenchyma.

5. Lignified fibres are common in the phloem of the woody species.

6. The cork cells have remarkably wide lumina and are very deeply seated, arising from the inner layers of the pericycle. This is true only of woody species and of the rhizomes of some herbaceous forms.

7. There is a continuous ring of sclerotic fibres in the pericycle.

8. Sclereides are absent from the Berberidaceæ, unless *Berberidopsis* be included in the order.

9. In some woody species spines are present, either epidermocortical or foliar in origin.

10. No endodermis is distinguishable save in *Akebia* among the Lardizabalaceæ.

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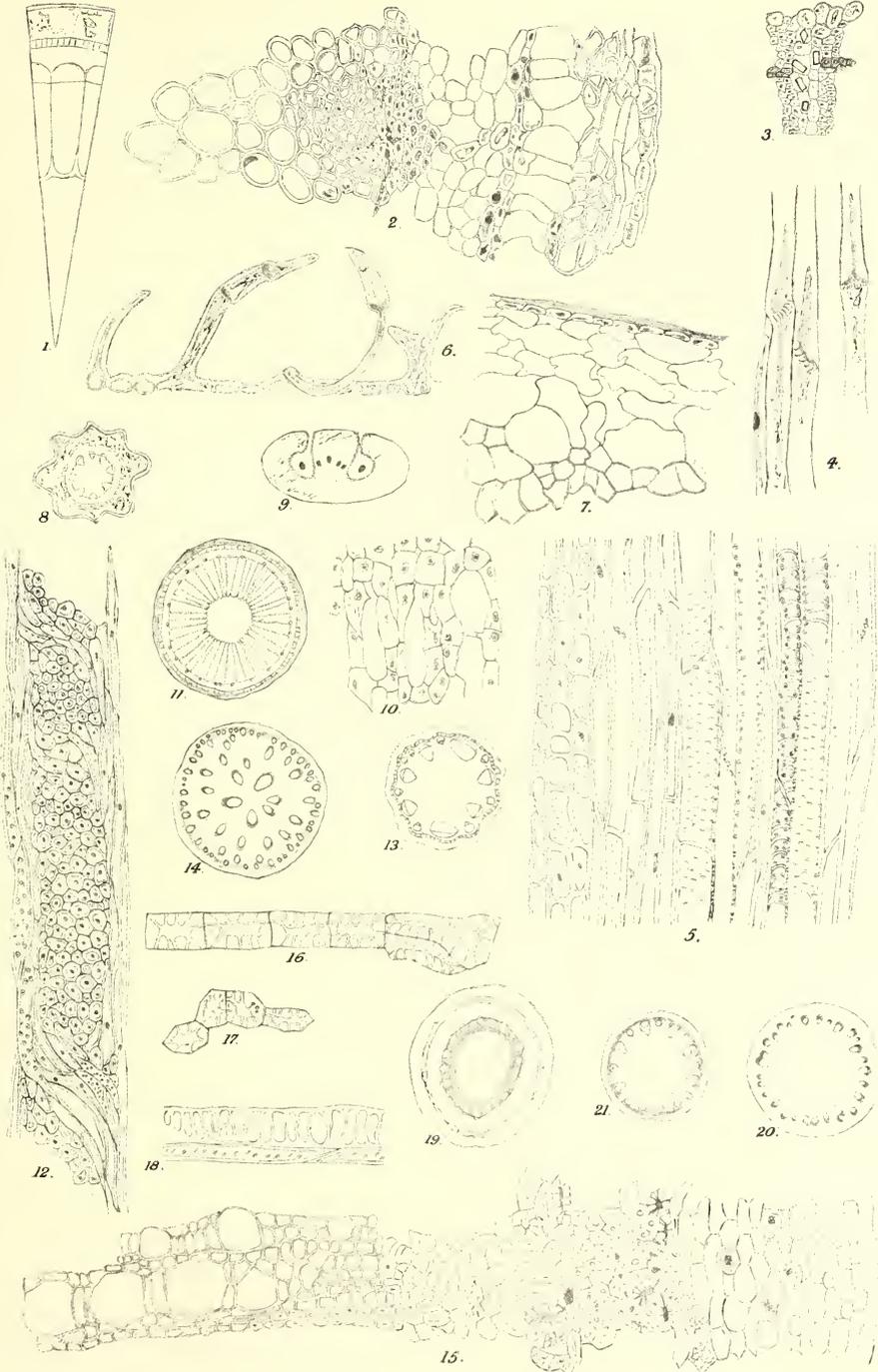
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## EXPLANATION OF PLATE.

- Fig. 1. Transverse section, stem of *Berberis vulgaris* (diagrammatic).  
Fig. 2. Transverse section, young stem of *B. vulgaris*, showing deep-seated ring of large cork cells. × 450.  
Fig. 3. Transverse section, stem of *B. elegans*, showing calcium oxalate crystals in medullary ray cells. × 450.  
Fig. 4. Longitudinal section, stem of *B. vulgaris*. Sieve tubes showing sieve plates and callus plugs. × 450.  
Fig. 5. Longitudinal section, stem of *B. vulgaris*. Xylem and medullary ray. × 450.  
Fig. 6. Epidermal cells and hairs of *B. Darwinii*. × 40.  
Fig. 7. Transverse section, stem of *B. aristata*, showing folding of the walls of sub-epidermal parenchyma. × 450.  
Fig. 8. Transverse section, stem of *B. angulosa* (diagrammatic).  
Fig. 9. Transverse section, spine of *B. atnensis* (diagrammatic).  
Fig. 10. Longitudinal section, stem of *B. empetrifolia*. External cortex, showing bridging of inter-cellular spaces. × 450.  
Fig. 11. Transverse section, stem of *B. Boschamii* (diagrammatic).  
Fig. 12. Longitudinal section, stem of *B. Walllichiana*, showing short blunt medullary rays. × 450.  
Fig. 13. Transverse section, rhizome of *Achlys triphylla* (diagrammatic).  
Fig. 14. Transverse section, stem of *Podophyllum Emodi* (diagrammatic).  
Fig. 15. Transverse section, stem of *Berberidopsis corallina*. × 450.  
Figs. 16 and 17. Transverse section and longitudinal section, stem of *B. corallina*. Stone cells of pericycle. × 450.  
Fig. 18. Longitudinal section, stem of *B. corallina*. Xylem elements with loose reticulate markings. × 450.  
Fig. 19. Transverse section, rhizome of *Vancouveria hexandra* (diagrammatic).  
Fig. 20. Transverse section, stem of *Hydrastis canadensis* (diagrammatic).  
Fig. 21. Transverse section, stem of *Jeffersonia dubia* (diagrammatic).



R. J. HARVEY-GIBSON and ELSIE HORSMAN on "The Anatomy of the Stem of the Berberidaceae."





XX.—Contributions towards a Knowledge of the Anatomy of the Lower Dicotyledons. III. The Anatomy of the Stem of the Calycanthaceæ. By Christine E. Quinlan, M.Sc., University College, Cork. *Communicated* by Professor R. J. HARVEY-GIBSON, C.B.E., D.L., M.A. (With One Plate.)

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The present paper is the third of a series of researches on the anatomy of the lower Dicotyledons undertaken with the object of seeing what, if any, aid anatomy might give in determining the point of origin of the so-called Monocotyledons. It deals more especially with the anatomical and histological peculiarities of the stem of the Calycanthaceæ.

#### HISTORICAL SUMMARY.

MIRBEL (1), in 1828, drew attention to the occurrence of four cortical vascular bundles in the stem of *Calycanthus floridus*, L., each consisting of phloem and xylem, inversely orientated, and with an arc of sclerenchyma on the outer margin. In 1833, GAUDICHAUD (2) found that, of the three petiolar bundles, the large median one enters the normal vascular ring, while the lateral bundles join the nearest cortical bundles; and his work was confirmed by TREVIRANUS (4). In 1836, LINDLEY (3), and, later, HENFREY (5), discovered this was common to all the Calycanthaceæ. In 1860, WORONIN (6) described the course of the cortical vascular bundles and their relation to the foliar bundles, confirming GAUDICHAUD as regards their mode of fusion, and pointing out that, at the node, a series of anastomoses occurs: (1) between the central vascular ring and each of the cortical bundles, (2) between the two opposite pairs of cortical bundles, (3) between the median and the lateral foliars at the base of the petiole, and (4) between the median foliar and the cortical bundles of the axis. In 1884, LIGNIER (7) showed that the median petiolar bundle gives off lateral branches which go to form the cortical bundles of the internode immediately superior, and pass out at a higher node.

In 1885, HÉRAIL (8) stated that the peripheral bundles of the stem of the Calycanthaceæ were pericyclar in origin and eventually become pushed out into the cortex, and that the peripheral bundles of each internode supply the lateral bundles of the leaves situated at a lower level, the median one coming directly from the central cylinder and receiving a branch from the lateral bundles. In 1887, LIGNIER denied the pericyclar origin of these bundles and stated that the bundles originate, and are always situated, in the cortex. In 1904, VAN TIEGHEM (9) held that in *Chimonanthus* the peripheral bundles were pericyclic, but in all species of *Calycanthus* purely cortical.

While investigators have paid attention chiefly to the peculiar anatomy of the Calycanthaceæ, the histological features have been generally overlooked; the present paper deals with the structure of the stem more especially from the histological standpoint, emphasising features not usually met with in Dicotyledons.

According to PRANTL (10), the order Calycanthaceæ includes two genera: Eucalycanthus and Chimonanthus. The former genus is primarily a native of North America, and comprises three species, viz. *Calycanthus floridus*, L., *C. fertilis*, Walt., and *C. occidentalis*, Hook and Arn. Chimonanthus is a native of Japan, and is monotypic, i.e. *Chimonanthus fragrans*, Lindl., a few varieties of which are in cultivation in Europe, var. *grandiflora* being the best known.

*Calycanthus fertilis* has been chosen for detailed examination; the other species will be referred to only in so far as they differ from it.

A transverse section through an internode of a very young stem (fig. 1) of *Calycanthus fertilis* shows the following arrangement of tissues: centrally a green heterogeneous pith, the cells becoming smaller towards the periphery; the vascular bundles arranged in an oval, in groups of four or five, and separated by well-marked medullary rays especially between the bundle groups. The xylem is not so well developed on the flanks of the oval. Outside the phloem is a small-celled tissue, representing the pericycle and endodermis, though neither of these layers is individually distinguishable. The cortex is differentiated into an inner layer of thin-walled green parenchyma with prominent intercellular spaces, and an outer layer of collenchyma. Some of the parenchyma cells of the cortex are differentiated into oil-secreting cells. In the cortex lie four vascular bundles with inverse orientation of the phloem and xylem and with a meristematic layer between. Each bundle is bordered externally by an arc of slightly thickened cells, which, later, become so sclerotic that their cavities are almost completely obliterated. External to the collenchyma is a unilamellar epidermis, bearing numerous elongated, unicellular hairs, whose walls are impregnated with silica. SOLEREDER (11) states that the cell bases are also silicified, but this I am unable to confirm. The hairs are often bent at right angles at their bases.

The larger central cells of the pith are faintly pitted and exhibit distinct foldings on their radial and longitudinal walls. The protoxylem consists of parenchyma, in which are scattered spiral, annular, and reticulate vessels and large spiral tracheides. The spiral thickenings are single. The cambiform cells are barely distinguishable, but, here and there, may be seen to consist of about two layers of cells not so elongated as the xylem parenchyma. The phloem consists chiefly of phloem parenchyma. Sieve-tubes and companion cells are present, but the sieve-plates are very inconspicuous. The companion cells are prominent and contain nuclei and granular contents. Usually three layers of parenchyma cells containing chlorophyll are intercalated between the phloem of the central cylinder and

the phloem of the peripheral bundle. The sieve-tubes in the latter are very numerous, but the phloem parenchyma is less abundant than in the central stele. Sieve-plates usually occur on the end walls, but one or two occur on the lateral walls also. The xylem of the peripheral bundle consists of spiral, annular, and reticulate vessels, and spiral tracheides, but there is no xylem parenchyma. On the outer side of the xylem lies a mass of elongated prosenchyma whose cells undergo sclerosis as age increases. Externally are several layers of cortical pitted parenchyma, while scattered in the parenchyma are large spherical oil-secreting cells (fig. 2). Outwardly the cortical parenchyma merges gradually into four or five layers of subepidermal collenchyma containing a few chloroplasts. Silicified bent unicellular hairs, their points directed towards the apex of the stem, lie deeply embedded among the epidermal cells. Stomata appear to be entirely absent.

As the shoot elongates, the outer cells of the pericycle become uniformly thickened and sclerotic in small isolated groups (fig. 5). These cells must not be confused with the sclerotic cells with U-shaped thickenings which one sees clearly in the layer continuous with the sclerenchymatous arc of the peripheral bundle. The fibres on the outer margin of the peripheral bundles also become strongly lignified, and the pits become extremely narrow canals. The sieve-tubes increase greatly in number, and tracheides with bordered pits and spiral thickenings appear. In the normal cylinder, the phloem parenchyma increases in volume and constitutes the greater part of the bast; pitted wood parenchyma is also present. The cortex and pith remain unaltered.

In the older stems all the vessels and tracheides of the xylem, as also the xylem parenchyma, become greatly lignified. Two kinds of tracheides are met with, viz. long narrow tracheides with pointed ends, whose walls bear uniseriate bordered pits, and larger but shorter tracheides with two or three longitudinal rows of bordered pits. In some, the pits become so elongated transversely that they appear scalariform. The bordered pits are either in longitudinal rows or scattered irregularly. Here and there, among these elements, are elongated, strongly lignified fibres without pits.

The medullary rays, seen in transverse section, are very numerous and uniseriate, and from three to five cells deep. The cell walls have numerous simple pits, or bordered pits on the side abutting on a tracheide; in a few cases pits are absent. Tyloses are frequent in the large pitted vessels. Most of the tracheides are intermediate between the elements with ordinary bordered pits and the scalariform tracheides so characteristic of Pteridophyta.

The secondary phloem shows a large development of phloem parenchyma and comparatively few sieve-tubes, while the sieve-tubes in the peripheral bundles are numerous and are accompanied by relatively little phloem parenchyma. The sclerotic cells of the peripheral bundles have greatly thickened walls, as have also the pericyclic fibres. The secondary cells are conspicuous, and show slight traces

of lignification. The cortical parenchyma, seen in transverse section, is arranged in definite layers, which readily separate on sectioning. The individual cells are connected by distinct pits in the walls. These pits are seen everywhere in the ground tissue, and become more noticeable as the tissue increases in age. The collenchyma cells are much thickened, and towards the periphery become flattened and merge into the subepidermal phellogen. The cork cells become elongated radially and show marked foldings on the radial walls, probably due to the pressure exerted by the growth of the internal tissues. Deposits of tannin are found in the dead epidermis, and particularly around the bases of the silicified hairs. Lenticels of the ordinary type are common.

The floral axis exhibits the same structure anatomically as the ordinary stem. On approaching the thalamus, the normal vascular ring divides into about fourteen distinct bundles. The pedicel bears two small opposite leaf-like bracts. The first pair of sepals are also opposite and decussate with the bracts. The leaf-trace bundles of the latter are similar in structure to those described below for the ordinary leaves. On nearing the thalamus the cortical bundles bifurcate, and one branch divides again. At this stage two of the vascular bundles of the central cylinder jut out at two opposite points into the peripheral ring, becoming the median vascular cords of the first sepals. Anastomosis occurs between the contiguous members of the last division of the peripheral bundles on the flanks. The occurrence of these anastomoses in the peripheral ring is very irregular; several may be seen in one axis, and none in another. When the first sepal is given off, it receives a median bundle from the central vascular ring, and two laterals from the peripheral ring; but, before entering the sepal, anastomosis takes place between the median and the lateral bundles, and between the lateral bundles themselves. Similar anastomoses occur at the points of origin of all sepals, petals, and stamens. The vascular cords supplying the carpels arise from the central stele only. They receive no strands from the peripheral ring. Every time a branch of a peripheral bundle passes out into a floral segment, the xylem and phloem, which were inversely orientated in the pedicel, become normally arranged by a revolution through an angle of  $180^\circ$ , while the sclerenchyma disappears from the peripheral bundles as they approach the thalamus.

The mode of entry of the leaf-trace bundles in *C. fertilis* is complicated. In the petiole, there may be five or seven bundles, one large median and one or two smaller laterals on each side. The laterals gradually decrease in number by joining the median or the extreme laterals, till there are, eventually, only three left. This is the condition found at the base of the petiole near its insertion on the axis. The vascular ring of the stem opens, and, as the leaves are opposite, two gaps occur at each node. The foliar gaps occur between the peripheral bundles. The median foliar bundle enters the central vascular system through the gap, and is accompanied by the vascular cords from the two axillary buds, which arrange them-

selves crescentwise, each joining the adjacent margin of the median bundle, thus forming a more or less continuous arc. This gradually approaches, and finally becomes inserted in, the central cylinder. Before doing so, however, the median foliar bundle gives off two lateral strands, one on either side. Each lateral strand divides into two segments, one of which joins the lateral foliar bundle, the other unites with the peripheral bundle of the axis. The lateral foliar bundle joins the peripheral bundle of the axis a little lower down, and has no connection with the central stele. Immediately after the median foliar bundle has joined the central cylinder and the laterals have united with the peripheral bundles, anastomosis takes place between the flanking peripheral bundles. The vascular strands of the foliar bundles are normally orientated, but the lateral segments, on approaching the peripheral bundles of the stem, become inverted. The arc formed by the median on entering the stem becomes less and less conspicuous as the node merges into the internode below, where the central cylinder becomes cylindrical once more.

The stem of *Calycanthus floridus* shows very little difference in external appearance from that of *C. fertilis*.

In transverse section it also resembles in all essential respects *C. fertilis*. The normal vascular bundles fuse to form a complete ring by an early development of an interfascicular cambium, leaving only narrow medullary rays between. These rays are only one cell wide, even in the young stem, and contain chloroplasts. The cambium ring is very conspicuous and four or five layers in thickness. Both in the normal vascular ring and in the peripheral bundles, crystals of calcium oxalate are deposited in radiating masses, either attached to the cell membrane or lying free in the cells. Double spirals are often met with both in the protoxylem of the central stele and of the peripheral bundles. Tracheides with bordered pits occasionally occur in the primary xylem. The sieve-tubes are very indistinct in the central bundles, but are clearly differentiated in the phloem of the peripheral bundles. Companion cells with dense contents are very prominent.

The secondary xylem consists mainly of reticulate tracheides with uni- or multi-seriate bordered pits, or with scalariform markings. The secondary xylem also includes lignified pitted parenchyma cells. SANIO (12) states that the walls of these cells become broken down by the disintegration of the membrane to form a mucilage or gelatinous layer which turns violet on treatment with iodine and bright crimson with phloroglucin and hydrochloric acid. As in *C. fertilis*, there are also lignified prosenchyma fibres without markings or pits, interspersed among the other elements, probably mechanical in function.

The peripheral bundles in older stems are surrounded by a layer of slightly sclerotised cells. The collenchyma cells have thick walls with canal-like pits. The walls of the cortical cells are also thickened, but not to so great an extent. The pericycle consists of isolated groups of sclerotic fibres between the phloem of the central stele and the parenchymatous cortex. Between the groups some of

the cells are thickened on the inner and lateral walls, and thus form a heterogeneous pericycle. The sclerotic groups themselves, however, never fuse to complete the pericycle, even in an old stem. In the old stem, traces of lignin are found in the walls of the oleiferous cortical cells. Secondary thickening of the cortex has its origin in the subepidermal region or the "exodermis" of VAN TIEGHEM, and the radial walls of the cork cells show well-marked foldings.

The pericyclic origin of the peripheral vascular bundles is seen more clearly in *C. floridus* than in *C. fertilis*. It has been shown that the cells with U-shaped thickenings occur between, and in some places in a direct line with, the uniformly sclerotic cells, and so form part of the pericycle. The sclerotic cells with U-shaped thickenings are also found in the layer of cells surrounding the peripheral bundles on the outside. Since the peripheral bundles are seen to be inserted between the outer layer of the pericycle and the phloem of the central stele, it may be concluded that they are pericyclic in origin.

The leaf-trace insertion on the whole resembles that of *C. fertilis*. The number of vascular bundles in the petiole varies, but is usually four or, more commonly, five. In no case did I find three bundles, as recorded by GAUDICHAUD. As a rule, in each petiole, there is one large median bundle and two smaller laterals on either side. The median bundle enters the vascular ring through the gap, but before doing so it gives off laterally two strands which join the lateral bundles, before the latter unite with the peripheral bundles of the axis. The lateral foliar bundles immediately flanking the median bundle unite sooner or later with the extreme lateral ones. The latter often unite with the peripheral bundle of the stem, before receiving the strand from the median foliar; and in some cases there may be a simultaneous fusion of the strands from the median foliar bundle, the lateral foliars, and the peripheral bundle of the axis. At a slightly lower level anastomosis takes place between the peripheral bundles on the flanks of the node. The axillary bud receives a very minute strand from the peripheral bundle of the stem. It passes inside the lateral foliar bundles and gives off a smaller strand to the younger bud on the outside.

The thalamus on examination shows a more regular arrangement of the bundles than in *C. fertilis*. Each of the peripheral bundles divides into two, and the number remains constant till the perianth segments begin to come off. After this many divisions take place which cannot be followed. Each sepal, petal, and stamen receives a median strand from the central stele and two laterals from the peripheral ring. There is always anastomosis between the median and the lateral bundles, but there is no transverse commissure between the laterals. The method of distribution is the same for all the floral segments except the carpels, which receive vascular cords from the central cylinder only.

The young stem of *C. occidentalis* in transverse section is practically identical with *C. floridus*, save that the endodermis is well defined and is easily recognised

by the abundance of starch grains in its cells. This endodermal layer encircles the so-called cortical bundles on the outside, showing clearly that they are pericyclic in origin. The pericycle consists of isolated groups of fibres. The cortex divides as usual into two layers, the inner containing numerous oleiferous cells. The epidermis bears silicified hairs, though not so numerous or so well developed as in *C. fertilis* or *C. floridus*.

In longitudinal section the primary xylem consists of annular, spiral, and reticulate vessels, and spiral tracheides, while tracheides with uni- or multiseriate bordered pits are very frequent in the secondary wood. Scalariform tracheides are not common. In the older wood the different varieties of tracheides give place almost completely to the peculiar tracheides described in *C. floridus* and compared by LIGNIER to those found in *Taxus*. Tyloses are frequent in these tracheides. The xylem parenchyma is small in amount and the medullary rays are uniseriate, consisting of cells containing abundant starch. They may be from twelve to sixteen cells deep. In the xylem their walls are pitted; in the phloem the walls are slightly thickened but bear no pits, and merge gradually into the pericyclic parenchyma.

In a one-year-old stem the sieve-tubes are scarcely distinguishable, either in the phloem of the central cylinder or in the peripheral bundles, though they are readily seen in both tissues of a second-year stem. In all cases, the fusiform companion cells are prominent. DE BARY (13) says, in describing the phloem of the peripheral bundles: "It only consists of soft bast and in the main, at least, of parenchymatous elements; sieve-tubes still remain to be sought for." HÉRAIL (8) makes no mention of sieve-tubes in the peripheral bundles, though LLOYD W. WILLIAMS (14) states that, in comparing the bast of the peripheral bundle with the bast of the normal vascular ring, both contain sieve-tubes and companion cells, but the sieve-tubes in the former are far more numerous than in the latter. I found sieve-tubes in both tissues, and I agree with LLOYD WILLIAMS as to the great difference in the number of sieve-tubes, and I would further draw attention to the difference in the size of the sieve-plates themselves.

Oleiferous cells occur frequently in the parenchymatous cortex but not elsewhere, though LIGNIER states that they occur in the pith and bast, and even in the cork underneath the old epidermis. He also states that the walls of the oleiferous cells are both lignified and suberised. Only in a few cases could I find traces of lignin. The periderm is formed in the secondary stem by the activity of an exodermal cambium. The walls of the cork cells outside the phellogen show marked foldings. Tannin deposits are found in the dried epidermis, and LIGNIER also finds resin. The cambial layer in the central cylinder is not so clearly marked as in *C. floridus*, and the same is true of the cambium of the peripheral bundles. The pith is heterogeneous, and its small lignified peripheral cells contain large starch grains. The vascular tissue, both of the central cylinder and the peripheral bundles, contains abundant radiating needles of calcium oxalate. LIGNIER finds them also in the

pith, where, he says, at least one needle may be seen in every cell. I found no trace of crystalline masses in the pith.

LIGNIER regards the irregularly thickened pericyclic fibres as an inner lignified layer of cortical parenchyma, and the uniformly sclerotic cells as the bast fibres. This can scarcely be correct. Both layers undoubtedly belong to the pericycle, as is evidenced by the fact that a well-defined endodermis is seen immediately outside. Both kinds of fibres form, in cases where they are developed, a layer continuous with the arc of sclerenchyma of the peripheral bundle. HÉRAIL states that the peripheral bundles, after differentiation from the pericycle, pass out into the cortex and remain there. This is not the case in any species of *Calycanthus*, even where the endodermis is not visible, since the sclerotic crest of the bundle is seen to be in direct continuity with the layer of pericyclic fibres; and where the endodermis is visible, it is situated on the outer, and not on the inner side of each bundle.

In the older stem the peripheral bundle, seen in transverse section, resembles in shape a wide sector of a circle, with the angle directed outwards. The rounded angle is filled with sclerenchymatous tissue; this crest is connected at each side with one of the isolated groups of pericyclic cells. It is in this region that the irregularly thickened cells most frequently occur; they are rarely seen interspersed among the ordinary pericyclic fibres, as is the case in *C. floridus*. The xylem occupies a semicircle immediately within the sclerenchyma, and consists of elements like those seen in the younger tissue of the central stele. There are no reticulate tracheides with bordered pits, nor wood parenchyma. The phloem forms two wings on the inner side, and is separated from the xylem by a V-shaped layer of cambium which gives rise to secondary tissue. The phloem is arranged almost in two strands; in fact, VAN TIEGHEM regards them as separate strands united by a common mass of xylem and sclerenchyma. Groups of sclerotic cells occur between the peripheral bundles and the central stele, among pericyclic parenchyma. The latter might easily be mistaken for cortical parenchyma, were it not that the endodermis stands out prominently after treatment with iodine, and completely separates the two layers.

A series of sections through the node shows the usual ramification of vascular strands. In addition, the peripheral bundle of the stem gives off a definite strand which passes inside the lateral foliar bundles towards the axillary buds. Here the inner bud receives the main strand, and gives off one very minute branch to the outer bud. These, later, become the peripheral bundles of the axillary branches, and always remain connected with the mother axis at the node.

The stem of *Chimonanthus fragrans* differs very little from that of *Calycanthus*.

A transverse section of a one-year-old stem shows the usual arrangement of vascular tissue. The epidermis bears numerous silicified hairs, which are short and stout, and inserted by broad bases between the ordinary epidermal cells. Very few show the bend so characteristic of *Calycanthus*. The cortex is divided into the usual two layers, one collenchymatous, the other parenchymatous. Here and there,

glandular cells occur, but they are not nearly so numerous as in *Calycanthus*. The cells of the innermost layer of the parenchyma contain abundant starch grains, and represent an endodermis, though in other respects they do not differ from the underlying cells. The endodermis surrounds the outer border of the peripheral bundles, leaving no doubt as to their pericyclic origin, though LIGNIER regards them as cortical. The peripheral bundles are elliptical in outline, and consist of an internal phloem followed externally by xylem, and a mass of sclerenchyma. The phloem is well developed, but does not form wings as in *Calycanthus*. The xylem is poorly developed. It consists entirely of annular, spiral, and reticulate vessels and a few spiral tracheides, there being no xylem parenchyma. Double spirals occur both in the vessels and the tracheides. The pericyclic layer consists of isolated groups of uniformly sclerotic fibres, situated immediately inside the endodermis. Cells with irregular thickenings are rarely seen in a first-year stem. Occasionally glandular cells are found in between the cortical stele and peripheral bundles. The phloem consists almost entirely of parenchyma, sieve-tubes and companion cells being few in number. Frequently, on the inner sides of the parenchyma cells bordering the inner margin of the peripheral bundles, radial foldings occur, usually extending about half way across the cell. Glandular cells are frequent in the bast, and the cambial layer is barely distinguishable. In the older parts tracheides with multiseriate bordered pits are found, but the pits are only faintly developed. Abutting on the protoxylem is a small-celled chlorophylliferous pith, merging into a central large-celled colourless pith. Oleiferous cells are found towards the periphery, but are rare, though VAN TIEGHEM states that they do not occur in the pith. Medullary rays are uniseriate and resemble closely those found in *Calycanthus*.

The pericyclic ring in stems two or more years old is completed by irregularly thickened sclerotic cells which fill up the gaps between uniformly sclerotic fibres, while the secondary xylem consists mainly of lignified fibres in which the tracheides are embedded. The commonest type of tracheide is that with bordered pits and spiral or reticulate markings, while tyloses are often found partly blocking their lumina. Xylem parenchyma is of rare occurrence in the old wood, though it is fairly abundant in the younger tissues.

The leaf-trace insertion differs slightly from that occurring in *Calycanthus*. There are three foliar vascular bundles, one large median, and two smaller lateral. Two gaps are formed on opposite sides of the vascular ring of the axis (*a*) immediately above the point of insertion of the petiole. Two buds are seen in the axil; the inner is large, the outer very small. At a lower level the inner bud receives a strand from the peripheral bundle of the axis (*b*), and the vascular tissue of the axillary buds arranges itself into two semicircles on either side. These fuse by their adjacent ends. A gap occurs first on the inner side, then on the outer side, and each half fuses with the vascular tissue of the central axis. Meanwhile, the peripheral bundles become elongated tangentially, and receive the lateral foliars as

they approach the axis (*e*). On the flanks, the peripheral bundles become elongated tangentially (*d*), and the median foliar bundle approaches and gives off two lateral strands which diverge and fuse with the peripheral bundles. The latter separate and gradually contract till they reach their normal size. The median foliar finally becomes inserted in the central vascular ring (*e, f*), and is eventually lost in the lower internode. The lateral foliar bundles, before joining the peripheral bundles, become inversely orientated. The same inversion takes place in the strands which leave the median foliar bundle to fuse with the peripheral bundles. The latter differ from those of *Calycanthus* in that they retain their sclerenchyma throughout the node.

#### SUMMARY.

The most noteworthy anatomical peculiarities in the structure of the stem of the Calycanthaceæ are as follows:—

##### 1. The occurrence of two basipetal axillary buds.

Two axillary buds occur in all the species of both genera. In *Calycanthus*, they expand into leafy shoots almost simultaneously, the outer being later in development. In *Chimonanthus*, the opening of the outer bud is delayed till the stem is in its fifth or sixth year.

##### 2. The occurrence of four vascular bundles in the pericycle.

These bundles were found in all the species examined. HÉRAIL states that they are situated in the cortex of *Calycanthus*, and that in *Chimonanthus* they originate in the pericycle and move out later into the cortex. LIGNIER holds that they are both cortical, while VAN TIEGHEM regards the bundles in *Calycanthus* as cortical, and those of *Chimonanthus* as pericyclic. So far as *Chimonanthus* is concerned he is correct, but in *Calycanthus* an endodermis encircles the peripheral bundles along their outer margins, and hence they must be pericyclic in origin. In *C. fertilis* and *C. floridus* the layer of pericyclic sclerotic cells is continuous with the arc of sclerenchyma bordering the bundles exteriorly, again demonstrating the pericyclic origin of these bundles. As already stated, the bundles are inversely orientated.

##### 3. The presence of a heterogeneous pericycle.

The pericycle consists of two kinds of fibres, viz. uniformly sclerotic fibres, and sclerotic cells with U-shaped thickenings. The latter are few in number in *Calycanthus*, but are very numerous in *Chimonanthus*. In *Calycanthus*, the groups of uniformly sclerotic fibres never fuse to form a continuous pericycle. In that genus, the irregularly thickened cells occur either in isolated groups or joined to the groups of uniformly thickened fibres. In *Chimonanthus*, the gaps between the groups of uniformly thickened cells are filled with the second type of sclerotic cells in the second and third years.

## 4. The pith is heterogeneous.

The periphery of the pith consists of a small-celled tissue containing chloroplasts. The central cells are large, and after the first year lose their contents.

## 5. Foldings in cell walls.

The radial walls of the first-formed cork cells are elongated, and, almost immediately after formation, show marked foldings (*cf.* 15), especially in the region outside the peripheral bundles. In *Chimonanthus*, the phloem of the central stele is crushed beneath the peripheral bundles, and the inner tangential walls show foldings. Foldings were also observed in the pith of *C. fertilis*.

## 6. The occurrence of oleiferous cells.

Glandular cells occur in the cortical parenchyma of all species of *Calycanthus*. In *Chimonanthus* they are found in the bast, the pericyclic parenchyma, and in the pith, as well as in the cortical parenchyma. In old stems the walls are slightly lignified.

## 7. The occurrence of pits on the walls of the cortical cells.

Pits invariably occur on the walls of the cortical cells both in the parenchyma and collenchyma.

## 8. The presence of unicellular silicified hairs.

These hairs occur on the epidermis. They are long and bent near the base in both *Calycanthus* and *Chimonanthus*.

## 9. The occurrence of scalariform tracheides.

Scalariform tracheides similar to those occurring in Pteridophyta are found in *C. fertilis*, *C. floridus*, *C. occidentalis*, and *Chimonanthus fragrans* var. *grandiflora*.

10. The occurrence of spiral or reticulate tracheides with bordered pits in the secondary xylem.

These are found in every species examined, except *C. fertilis*. In *C. occidentalis* they are very abundant, to the exclusion of all other elements except the libriform fibres. The bordered pits may be uniseriate or multiseriate. The lumina of these tracheides are often blocked by tyloses.

## 11. Multiseriate bordered pits.

Tracheides with multiseriate bordered pits are frequent in *C. fertilis*, *C. floridus*, and *Ch. fragrans* var. *grandiflora*. Here tyloses are also frequent.

## 12. Double spirals in the primary tissues.

Double spiral thickening is seen on the walls of the vessels of *C. floridus* and *Ch. fragrans*; they also occur on the tracheides of the latter.

## 13. The occurrence of lateral sieve-plates.

Lateral sieve-plates were found in *C. fertilis*, *C. occidentalis*, and *Ch. fragrans* var. *grandiflora*.

## 14. Anastomosis at the nodes.

At the node the vascular system is complicated. In all species there are transverse strands uniting the peripheral bundles on the flanks. The median foliar bundle at the base of the petiole gives off lateral strands which unite with the lateral foliar bundles. The peripheral bundles give off a minute branch which enters the axillary buds, in all species except *C. fertilis*, in which it appears at a later stage of development.

## 15. Peculiarity of leaf-trace entry.

The vascular ring of the axis opens to admit the median foliar bundle, while the lateral foliars unite with the nearest peripheral bundles. Each of the axillary buds possesses a vascular ring, which divides into two crescentic masses. The crescents belonging to the outer bud fuse laterally with the respective crescents of the inner bud. In *Calycanthus*, each set unites with the arc of the median foliar bundle, before its insertion into the ring of the central stele; in *Chimonanthus*, they unite laterally with the central vascular tissue on each side of the gap, separating on the outer side to admit the median foliar bundle.

## 16. Inversion of the lateral foliar bundles at the node.

On entering the mother axis at the node, the lateral foliar bundles, when fusing with the peripheral bundles, become inversely orientated. This change in orientation takes place also in the lateral strands given off by the median foliar bundle.

## 17. Anastomosis in the floral axis.

In *C. fertilis* and *C. floridus*, each floral segment, except the carpels, receives from the central vascular ring a median strand, and from the peripheral ring, two smaller lateral cords. The median cord gives off two branches which join the lateral cords; in *C. fertilis*, there is also anastomosis between the lateral cords. The carpels receive branches from the central cylinder and not from the peripheral ring.

I should like to express my thanks to Professor R. J. HARVEY-GIBSON, C.B.E., of Liverpool University, at whose suggestion the work was undertaken, for his constant help and advice; to Professors B. E. DUKE and HARTOG of University College, Cork, and also to Professor H. H. DIXON, F.R.S., and Sir FREDERICK MOORE, for supplies of material.

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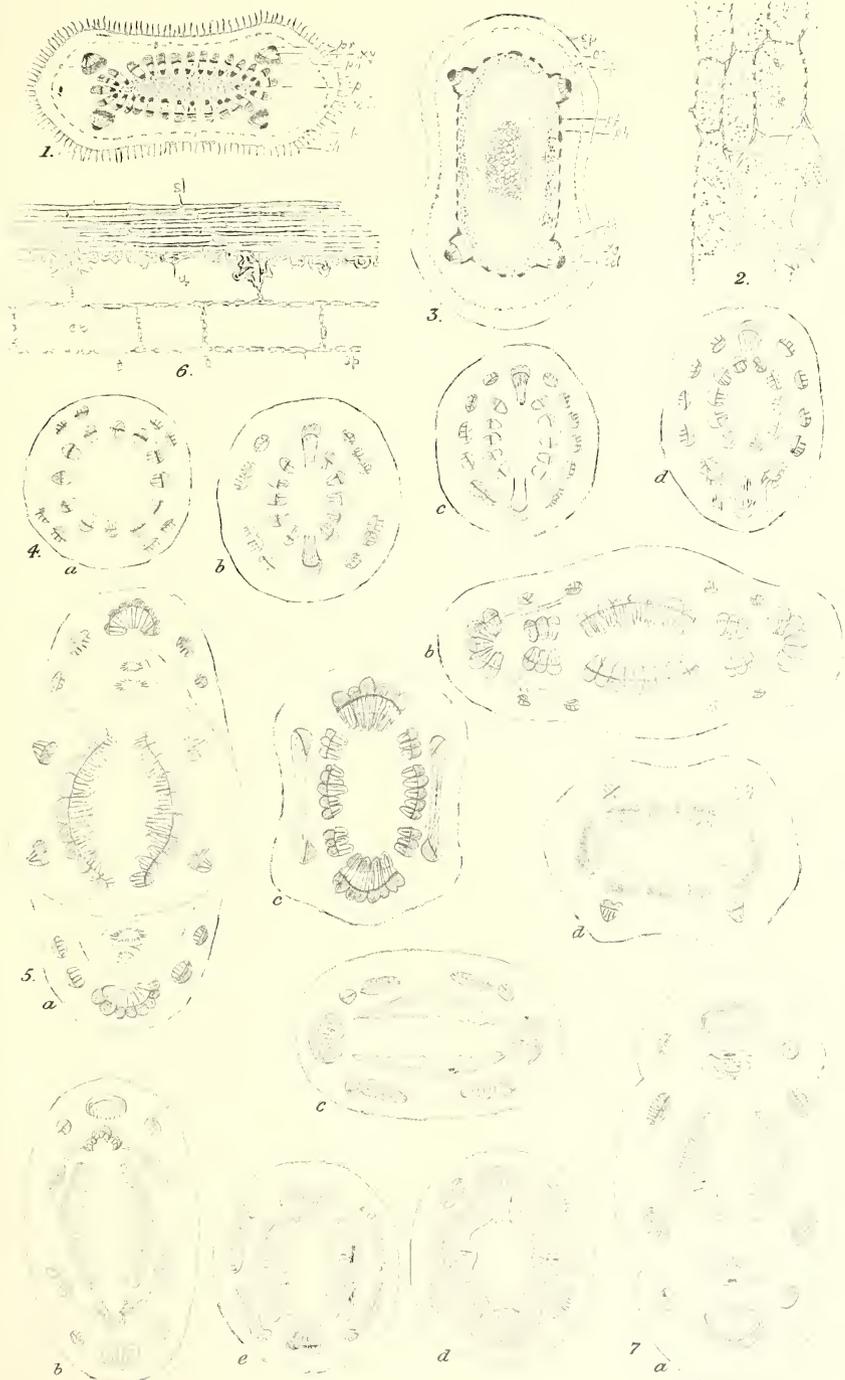
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## EXPLANATION OF PLATE.

- Fig. 1. Transverse section through internode of a very young stem of *C. fertilis* (L).
- Fig. 2. Longitudinal section through parenchymatous cortex of *C. fertilis* (H).
- Fig. 3. Transverse section through region below node of *C. fertilis* after elongation (L).
- Fig. 4. *a-d*, series of sections through thalamus of *C. fertilis* (L).
- Fig. 5. *a-d*, series of sections through node of *C. fertilis* (L).
- Fig. 6. Longitudinal section of secondary stem of *C. floridus*, showing U-shaped cells and fibres of peripheral bundle (H).
- Fig. 7. Successive sections of node of *Ch. fragrans*, showing leaf-trace entry (L).



Miss CHRISTINE E. QUINLAN on "The Anatomy of the Stem of the Calycanthaceae."



C. E. Q. del.



XXI.—The Comparative Myology of the Shoulder Girdle and Pectoral Fin of Fishes. By Captain E. W. Shann, B.Sc., Oundle School. *Communicated by* Professor W. C. M'INTOSH, F.R.S. (With Four Plates and One Figure in the Text.)

(MS. received October 16, 1918. Read February 3, 1919. Issued separately September 26, 1919.)

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INTRODUCTION.

Some months ago it was suggested that I should publish my thesis in its unfinished state. I refrained from doing so at that time, as I was unwilling to allow my work to appear until it was ready for publication. When it became apparent that the war might continue indefinitely, I decided to publish the thesis in such a form as the exigencies of the case would allow.

For some years I had been fascinated by that elusive problem, the evolution of the pentadactyle limb of the higher Vertebrates. An extensive list of literature bearing directly or indirectly on this subject was gathered, and notes were made from upwards of a hundred monographs. It soon became clear that a necessary preliminary to the solution of the problem was a thorough knowledge of the limbs of fishes and their manifold modifications. The hind limb had been most ably handled by DAVIDOFF as early as 1873, and the skeleton of the fore limb had been extensively treated by BRAUS, GEGENBAUR, OWEN, PARKER, and others; what still remained in a very unsatisfactory state was the musculature of the fore limb. Numerous authors had dealt with this latter subject, notably BRAUS (11), FURBRINGER (31, 32, 33), HAMBURGER (42), HARTMANN (44), HUMPHRY (50, 51, 52), JAQUET (55), M'MURRICH (60), MARION (62), OWEN (73), TIESING (87), and VETTER (88), but few of these had treated it from the comparative standpoint; moreover, the nomenclature was found to be so much at variance as to obscure probable homologies on the one hand, and, on the other, to suggest homologies where none in all probability exist. My object, then, became to elucidate the musculature of the fore limb of fishes.

I am indebted to Professor GRAHAM KERR for specimens of *Lepidosiren* and *Polypterus*, and to Dr W. M. TATTERSALL for *Periophthalmus*; the remainder of the types, with the exception of a few from my own collection, were generously placed at my disposal by Professor W. C. M'INTOSH, from the Zoological Department and Museum at St Andrews University. I also wish again to record my indebtedness to the Carnegie Trust, which provided me with the low-power Zeiss binocular microscope under which many of my dissections were carried out.



KEY TO THE MUSCULATURE OF THE PECTORAL ARCH AND FIN IN ELASMOBRANCHII.

		GEGENBAUR.	HUMPHRY.	MARION.	OWEN.	WIEDERS-HEIM.	VETTER.	Remarks.
Posterior fixation muscles.	(a) Retr. lat.-dors. pect.	...	...	...	...	...	...	Not always present.
	(b) R. lat.-vent. pect.	Lat.-scapul.	Serratus.	...	Neuro-lat.	...	...	Serratus of BRAUS.
	(c) R. mes.-vent. pect.	...	...	...	...	...	...	M. du ventre of JAQUET.
	(i) Superior	...	Latiss. dors.	...	...	...	...	
	(ii) Medius.	...	Axill. portion.	...	...	...	...	
	(iii) Inferior	...	Pectoralis.	...	...	...	...	
Anterior fixation muscles.	(a) Protr. lat.-dors. pect.	...	...	...	...	...	...	Not always present.
	(b) P. lat.-vent. pect.	...	...	...	Protr. scap.	...	...	Wanting in Holocephali.
	(c) Mesio-vent. derivs.	...	...	...	...	...	Trapezius (pars).	Trapezius of JAQUET.
	(i) Levator pect.	Trapez. (pars).	Levator scap.	Trapez. (pars)	...	...	...	
	(ii) Coraco-arc. comm.	...	Cervic. prof. (pars).	Coraco-arc. comm.	...	...	...	
	(iii) Coraco-branch.	...	Deepest part of c.p.	Coraco-branch.	...	Coraco-branch.	Coraco-branch.	
	(iv) Coraco-hyoideus	...	Cervic. prof. (pars).	Coraco-hyoid.	...	Coraco-hyoid.	Coraco-hyoid.	
(v) Coraco-hyomandib.	...	...	Coraco-hyomandib.	...	...	...	Only in Raia.	
	(vi) Coraco-mandib.	...	...	Coraco-mandib.	Depressor-mandib.	Coraco-mandib.	Coraco-mandib.	
Fin muscles.	(a) Adductor.	...	...	...	...	...	...	
	(i) Superficialis.	...	...	...	...	...	...	
	(ii) Profundus.	...	...	...	...	...	...	
	(b) Abductor.	...	...	...	...	...	...	
	(i) Superficialis.	...	...	...	...	...	...	
	(ii) Profundus.	...	...	...	...	...	...	

I. Selachii.

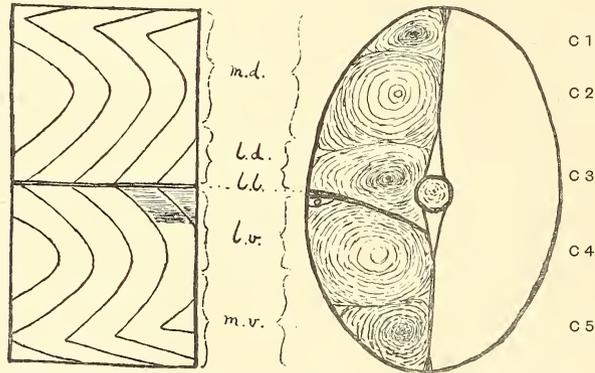
(*Scyllium canicula*, *Galeus canis*, *Acanthias vulgaris*, *Rhina squatina*,  
*Raia clavata*.)

I. SHOULDER GIRDLE.

(1) *The Lateral Muscle.*

Throughout its length the lateral muscle of Selachians is divided into a dorsal and a ventral moiety by a horizontal septum running from the lateral line to the transverse processes, and, further back, to their equivalents, the hæmal arches. In the dorsal moiety of the tail region (text-fig. 1) the myocommata may be traced superficially from the mid-dorsal line, running first forwards, then sharply backwards, then gently forwards again; following the same myocommata through the ventral moiety, they are seen to run first backwards, then gently forwards, lastly sharply backwards. On examining a transverse section of the tail, it is seen that the myomeres enclosed

by the above-noted myocommata form a series of concentric cones. In all, five such series of cones occur (C 1-5), of which the dorsalmost have their apices directed forwards, the next have their apices directed backwards, and so on in alternate order. This is clearly seen in the well-known diagram of *Scyllium canicula* in MARSHALL and HURST'S *Practical Zoology*; but the completeness of the division at the horizontal septum is not adequately brought out, nor is the position of the lateral-line nerve indicated. This occupies the furrow between the third and fourth series of cones. The directions taken externally by the myocommata are manifestations of the internal conformation. There is an apparent incongruity in that, though three series of



TEXT-FIG. 1.—Diagram of left lateral view of caudal region of *Scyllium* compared with a cross-cut of the same region seen from the posterior aspect.

In the lateral view the deep portion of the l.d. muscle, which, owing to the obliquity of the so-called "horizontal septum," underlies the l.v. muscle, is shown by shading in the two posterior myomeres.

C 1-5. Muscle cones: 1, concave; 2, convex,  
and so forth alternately.  
l.d. Latero-dorsal muscle.  
l.l. Lateral line.

l.v. Latero-ventral muscle.  
m.d. Mesio-dorsal muscle.  
m.v. Mesio-ventral muscle.

complete cones are seen in section in the dorsal moiety, only two and a half cones appear in corresponding areas on the surface. This incongruity is explained by the fact that the ventral moiety overlaps the dorsal to a certain extent; if the ventral moiety be dissected away from the dorsal, the myocommata of the latter are found to take a sharp bend backwards in the hidden area, thus completing the superficial manifestation of the third, anteriorly directed, series of cones (see text-fig. 1).

Let us now trace these muscles forwards to their insertions. The series of cones are indissolubly connected up to their insertion on the skull, though the upper two were designated mesio-dorsal (M.D.) and the lower one latero-dorsal (L.D.) portions respectively of the lateral muscle by HUMPHRY (51), who distinguished them by the directions of their superficial fibres. While agreeing with MAURER (*Morph. Jahrb.*,

1892) that this division of the dorsal moiety into mesio-dorsal and latero-dorsal portions has no morphological value, I have found it sufficiently useful for descriptive purposes, and it is retained under this proviso.

The ventral moiety in the anterior region is much modified owing to the presence of the abdominal cavity, whose walls it forms. The conical structure is almost lost, though, as we shall see later, evidence of it is retained in the lateral walls. The two portions described in the tail region are still recognisable externally by their myocommata. Internally there is, however, a much closer relationship between the lower half of the C 4 section and the C 5 section than exists between the two halves of the C 4 section in the anterior region. This led MAURER to follow HUMPHRY in his designation of the latero-ventral (L.V.) and mesio-ventral (M.V.) portions of the ventral moiety, the division being indicated in text-fig. 1. It is seen, then, that the latero-ventral portion comprises the upper half of the C 4 section, while the mesio-ventral portion comprises the lower half of the C 4 section together with the entire C 5 section.

In the latero-ventral portion the fibres throughout their depth run approximately parallel to the long axis of the body, the ventral limit of the muscle being defined externally by the backward slope of the myocommata, and internally by the distal extremities of the ribs. In the mesio-ventral portion the fibres run obliquely from downwards anteriorly to upwards posteriorly, but their obliquity gradually disappears as the ventral surface is reached, till they come to lie parallel to the long axis of the body, in which condition they reach the ventral septum which separates them from their fellows of the opposite side. These two superficial areas of the mesio-ventral portion were declared by MAURER (*ibid.*) to be the homologues of the obliquus internus and rectus respectively of the Amphibia. Moreover, on dissecting away the superficial oblique fibres, MAURER observed a second layer of oblique fibres, which took the opposite direction (namely, from upwards anteriorly to downwards posteriorly), and this layer he took to represent the transversus of the Amphibia. HUMPHRY also noted this stratification of the mesio-ventral portion. There is, however, no septum between these two layers; indeed, they pass by gradual transition one into the other. I have given in detail elsewhere\* my reasons for regarding this pseudo-stratification of the lateral muscle in the anterior region as a result of the conical conformation that occurs posteriorly.

### (2) *The Posterior Muscles.*

The lateral muscle when it reaches the pectoral girdle becomes interrupted in its course by that structure, either throughout its depth or in the superficial region only. The portions of the lateral muscle which are thus attached to the girdle constitute its posterior system of muscles, and, from the nature of their position, act as retractors.

\* *Proc. Zool. Soc.*, 1914, pp. 319 *et seq.*

They will be described in terms of the division of the lateral muscle which were advanced in the preceding section, as follows:—

- (a) Retractor latero-dorsalis pectoralis.
- (b) R. latero-ventralis pectoralis.
- (c) R. mesio-ventralis pectoralis :
  - (i) Superior.
  - (ii) Medius.
  - (iii) Inferior.

(a) *Retractor latero-dorsalis pectoralis (r.l.d.p.)*.—I can find no mention of this muscle in the works of previous authors. HUMPHRY, whose observations were based on *Mustelus lævis*, was of opinion that no fibres of the latero-dorsal portion are inserted on the tip of the scapula. The latter, he says (51, p. 272), “projects in between the fibres of the dorsal muscle, where it terminates in a ligament which is lost in one of the transverse septa.”

After the examination of a considerable number of specimens of *Scyllium*, it still remains doubtful whether this muscle may be regarded as present in that form. It is usually absent, the tip of the scapula being embedded in a pocket of connective tissue; but in certain cases a few fibres of the latero-dorsal portion undoubtedly took origin on the inner aspect of the scapular horn. In the one example of *Galeus* dissected no such fibres were observed.

It is in the compressed Selachians that this muscle attains considerable development. In *Rhina* it is well marked in the superficial area, while in the Rays the latero-dorsal portion originates in a tendon from the inner aspect of the postero-dorsal angle of the scapula.

In the Rays the outer section of the mesio-dorsal portion (C 2 section in text-fig. 1) is firmly attached to the postero-ventral aspect of the cartilage which joins the scapula to the vertebral column; while the dorsalmost section (C 1) of the mesio-dorsal portion runs freely beneath the said cartilage to its attachment on the chondrocranium. In these fishes, moreover, there is very little trace of myocommata in the anterior region of the lateral muscle, so that the fibres run uninterruptedly in longitudinal series. OWEN speaks collectively of the whole dorsal moiety of the lateral muscle in Batoids (*Torpedo*), which has been resolved above into its three constituent parts, as the “neuro-medial mass.”

(b) *Retractor latero-ventralis pectoralis (r.l.v.p.)*. Neuro-lateral muscle, OWEN; *Serratus*, HUMPHRY; *Latero-scapularis*, GEGENBAUR.—HUMPHRY observed in *Mustelus* that the scapula lies upon the latero-ventral portion, its lower edge being connected with one of the transverse septa of this muscle; moreover, that some of the fibres of the muscle pass into its under surface, constituting a “serratus.”

In *Scyllium*, *Galeus*, and *Acanthias*, the superficial fibres of the latero-ventral portion are attached to the posterior border of the scapula, while a few of the deeper

fibres are attached to its inner aspect; these constitute the retractor latero-ventralis pectoralis, and are distinguished by their peculiar dark colour. In actuality this muscle is more or less covered by the muscle next to be considered—the r.m.v.p. superior.

In the above types the muscle under discussion is divided by a fascia from the next of the series of retractors. In Rhina, on the contrary, there is no such distinction, the r.l.v.p. passing conformably into the r.m.v.p.

In Raia this muscle is present as a thin ribbon attached to the postero-ventral aspect of the scapula external to the lateral nerve. It differs from the above types in that it is entirely interrupted by the scapula, no part of it running forward beneath that cartilage.

(c) *Retractor mesio-ventralis pectoralis (r.m.v.p.)*.—The mesio-ventral portion encounters in its upper reaches the fin, and in its lower reaches the coracoid portion of the pectoral girdle, and is interrupted throughout its depth by these structures. It is more or less readily divisible into three regions of insertion: (i) superior—from the scapula and upper surface of the fin; (ii) medius—from the axil of the fin; and (iii) inferior—from the coracoid and under surface of the fin.

(i) R.m.v.p. superior. Latissimus dorsi, HUMPHRY; Serratus, BRAUS (14).

HUMPHRY described this muscle in *Mustelus* as follows: "It is inserted into the scapular part of the girdle, and expands upon the dorsal surface of the fin, reaching to its anterior edge. Upon the fin it lies upon, and to some extent blends with, the proper muscle of the fin."

I find that this condition obtains in *Scyllium*, *Galeus*, and *Acanthias*. The fibres run obliquely throughout the depth of the muscle upwards from their insertion; the muscle never attains a great thickness. If we take HUMPHRY'S description of the insertion, the origin is found to be, dorsally, from the surface of the r.l.v.p., while, ventrally, the fibres are continuous with those of the upper section of the mesio-ventral portion of the lateral muscle. Arching upwards, the end-line of the fibres extends as far up the side as the lateral line a short distance (about 10 mm. in *Scyllium*) behind the girdle. Posteriorly, the r.m.v.p.sup. rapidly diminishes.

In *Raia* this muscle does not cover the surface of the fin, but finds its insertion along the upper posterior rim of the metapterygium, as well as upon the scapula.

(ii) R.m.v.p. medius. Axillary portion, HUMPHRY.

That area of the mesio-ventral portion of the lateral muscle which meets the articular region of the pectoral fin is here implied. The fibres run obliquely in the same direction as those of the r.m.v.p.sup. The muscle is sometimes (*Scyllium*, *Galeus*) separated at its insertion from the last-named by a patch of connective tissue, in which case the muscle appears to concentrate upon a limited area of the coracoid just in front of the glenoid border. In *Galeus* and *Mustelus* (HUMPHRY) the insertion is more extensive and spreads upon the axillary aspect of the fin muscles, both

abductor and adductor, as well as upon the scapula (Galeus), in addition to the typical insertion.

The Rays differ from the shark-like types in that in them this muscle is inserted along the whole length of the metapterygium, beneath the r.m.v.p.sup., as well as to the scapular and coracoid portions of the girdle.

(iii) R.m.v.p. inferior. Pectoralis, HUMPHRY; Rectus(?).

This muscle is confined to the ventral aspect, and is very constant in form throughout the Selachii. In appearance it recalls the rectus of higher Vertebrates. It arises from the posterior border of the coracoid, and usually spreads to a slight extent over the abductor muscles of the fin. For a short distance behind its origin this muscle is separated by a low ridge from the axillary portion of the lateral muscle which has been described above.

### (3) *The Anterior Muscles.*

The anterior muscles which act upon the shoulder girdle are derived from the more or less modified forward prolongations of the lateral muscle.

The deeper fibres of the dorsal moiety and of the latero-ventral portion of the ventral moiety are continued forwards beneath the scapular region of the girdle, except in the Skates and Rays, and are still recognisable up to their points of origin on the chondrocranium; the superficial fibres in these areas were observed to be interrupted by the girdle. As these interrupted fibres behind the girdle serve as retractors of that structure, so their anterior homologues serve as protractors. The anterior fibres of the mesio-ventral portion are modified to such an extent by the development of the visceral arches that they require special consideration. The anterior muscles of the pectoral girdle will be dealt with in the following order:—

- (a) Protractor latero-dorsalis pectoralis.
- (b) Protractor latero-ventralis pectoralis.
- (c) Muscles derived from the mesio-ventral portion of the lateral muscles:
  - (i) Levator pectoralis.
  - (ii) Coraco-arcualis communis.
  - (iii) Coraco-branchiales.
  - (iv) Coraco-hyoideus.
  - (v) Coraco-hyomandibularis.
  - (vi) Coraco-mandibularis.

(a) *Protractor latero-dorsalis pectoralis (p.l.d.p.)*.—This muscle has, so far as I am aware, received no specific designation from previous writers. When present, it is derived from the interrupted superficial fibres of the latero-dorsal portion of the lateral muscle, which, arising from the anterior border of the scapula, are inserted immediately into the main mass of that muscle. It is necessary to make the proviso “when present,” for this muscle is developed in precisely the same degree as its equivalent the r.l.d.p.

Now, it has been seen that the latter is absent in *Mustelus* (HUMPHRY) and, at least, in some specimens of *Scyllium*, and in these cases the p.l.d.p. is also wanting.

In *Rhina*, where the r.l.d.p. is well marked, the p.l.d.p. is also well developed, taking origin by a tendinous sheet from the knob-like extremity of the scapula.

In *Raia* the anterior border of the cartilage which joins the scapula to the vertebral column is wider than the posterior border. For this reason all the fibres of the dorsal moiety of the lateral muscle which are attached anteriorly to the pectoral girdle take origin on the said cartilage.

(b) *Protractor latero-ventralis pectoralis* (p.l.v.p.). *Protractor scapulæ*, OWEN.—Actually the p.l.v.p. is overlain near its insertion by the levator pectoralis and, further forward, by the superficial branchial muscles; so that only a very small portion of it is visible without dissection (at its insertion). In *Scyllium*, *Galeus*, *Acanthias*, and *Rhina* this muscle shows marked constancy, and the following description is applicable to any of these types.

Immediately below the lateral line fibres are inserted into the outer and inner aspects of the anterior border of the scapula. Tracing these fibres forwards, after reflecting the overlying muscles noted above, they are found to take origin from the deeper fibres of the latero-ventral portion of the lateral muscle. Thenceforward the entire muscle is continued as a dorso-ventrally compressed mass which terminates in a tendinous insertion on the base of the chondrocranium. It is familiar to all who have had occasion to dissect the Dogfish as that muscle which separates the lateral nerve from the anterior cardinal sinus.

In *Raia*, though very much reduced, this muscle is present as a triangular strip, whose apex is inserted on the ventral aspect of the anterior upper portion of the scapula, while its base takes origin along the outer rim of the great lateral process of the first vertebra. The muscle was described by MARION (62) as "portion C of the trapezius."

Doubtless the great development of the vertebral process in *Raia* accounts for the fact that no part of this muscle reaches the cranium, which is the case in the shark-like forms.

(c) *Muscles derived from the mesio-ventral portion of the lateral muscle.*

(i) *Levator pectoralis* (l.p.). *Levator scapulæ*, HUMPHRY; *Trapezius* (pars), VETTER, GEGENBAUR, MARION.

The levator pectoralis is a compact triangular muscle whose base runs along the lateral septum from just in front of the scapula to the level of the third branchial arch. Its apex is curved slightly forwards, so that the posterior side of the triangle is slightly convex and the anterior slightly concave. The posterior convex border is inserted into the outer face of the scapula, which is usually grooved (markedly in *Acanthias*) to receive it. The body of the l.p. forms the outer wall of the anterior cardinal sinus.

The above description holds good for all the shark-like types. In *Raia* the l.p. is also present, though considerably reduced in extent.

The origin of the levator pectoralis, whether in the Sharks or Rays, is continuous anteriorly with that of a small muscle which runs to the last branchial arch; these two muscles constitute the trapezius of earlier writers, which from its superficial position and double function has received abundant notice.

(ii) *Coraco-arcualis communis* (c.a.c.). *Cervicalis profundus* pars, HUMPHRY; *Coraco-arcualis communis*, MARION.

On the ventral aspect of Elasmobranch fishes, anteriorly to the pectoral girdle, the lateral muscle is broken up into a complex series of separate muscles coming from the branchial, hyoid, and mandibular arches to be inserted on the coracoid portion of the girdle. These muscles, however, anastomose to a greater or less extent before reaching the girdle; so that a pair of muscle masses, derived from the separate portions of each side, occur immediately in front of that structure on either side of the mid-ventral line; each of these is named *coraco-arcualis communis*. The anastomosis spoken of above is not gradual, but takes place at a well-defined junction, namely, at a strong fascia—the coraco-arcual septum. The *coraco-arcuales communes* form internally the floor of the pericardium.

In *Scyllium* the c.a.c. is intercepted by four transverse myocommata, which enhances its resemblance to the portion of the lateral muscle immediately behind the coracoid—the retractor mesio-ventralis pectoralis inferior. HUMPHRY regarded this muscle, which he designated, together with the coraco-hyoideus (to be described below), *cervicalis profundus*, as the anterior continuation of the “pectoralis” (= r.m.v.p. inf.); moreover, he adds that the *cervicalis profundus* “presents transverse septa corresponding in number and position with the branchial cartilages.” The former surmise is highly probable, since HUMPHRY observes that this muscle “extends with the septum for some little distance upon the ventral aspect of the fin,” and a similar condition has been noted above in treating of the insertion of the r.m.v.p.inf.; in fact, the lateral range of these two muscles on either side of the median line at the level of their insertions on the girdle is almost identical. With regard to the transverse septa recorded by HUMPHRY for *Mustelus*, it is to be supposed that the most anterior of these is the coraco-arcual septum, while the remaining four are equivalent to the four myocommata which have been noted in *Scyllium*; they thus correspond in number to the branchial arches, but, in the latter type, they cannot be described as corresponding in position. The coraco-arcual septum in *Scyllium* is wedge-shaped, the thin edge of the wedge extending in a horizontal plane between the coraco-mandibularis and coraco-hyoideus on the ventral aspect, and the first coraco-branchialis on the dorsal aspect.

In *Galeus* the *coraco-arcuales* are exceedingly short, and are not traversed by distinct myocommata. *Acanthias* differs from the foregoing types in the considerable

length of these muscles, which extend fully one-third of the distance between the girdle and mandible; here again the muscles are divided by four myocommata, which observation is corroborated by MARION, though VETTER noticed only three. MARION's remark that the muscle in question is attached (in part) to a "fascia dorsal to the origin of the ceratohyal" is unintelligible, unless "ceratohyal" is a misprint for "coracohyal" (*i.e.* the coraco-hyoideus muscle), in which case the remark is accurate enough; the coraco-arcualis is very far removed from the hyoid arch.

A marked deviation is found in the case of Rhina. The coraco-arcuales are of enormous strength; they extend half the distance between the girdle and the mandible, and, in the single specimen examined, are traversed by nine myocommata.

In Raia the coraco-arcuales are very thin straps of muscle which only touch one another at their anterior extremities; they extend not quite half the distance between the girdle and the mandible. Their insertions on the coracoid are widely separated by the coraco-mandibularis, which in this form is inserted directly on the coracoid in the middle line. In no specimen have I been able to identify myocommata. In TIESING's work the *c.a.c.* are figured for Torpedo, Rhinobatis, and Raia, though no description is given in the text; no trace of myocommata occurs in these figures.

(iii) Coraco-branchiales (*c.br.*). Deepest portion of *cervicalis profundus*, HUMPHRY; Coraco-branchialis, WIEDERSHEIM, MARION.

The coraco-branchiales occur with marked constancy in the Selachians as a series of muscles which, inserted by separate tendons on the branchial arches, traverse the lateral walls of the pericardium to take origin on the coraco-arcual septum and on the coracoid cartilage. In the region of their insertion these muscles form columnar masses, but near their origin the distinct muscles become more or less fused with one another and become thinner and flatter in appearance. In the shark-like forms the *c.br.* bear a constant relationship to the afferent branchial arteries; the fused trunk of the first and second of these arteries appears immediately in front of the first coraco-branchialis muscle (*i.e.* in the space between it and the coraco-hyoideus), the third artery appears between the second and third *c.br.*, the fourth between the third and fourth *c.br.*, and the fifth between the fourth and fifth *c.br.*

Although Scyllium is perhaps the commonest fish to be dissected in the laboratories of this country, its coraco-branchial musculature, so far as I am aware, has not hitherto received any adequate attention. It differs markedly from that of the Piked Dogfish (*Acanthias*), which has been taken in hand by VETTER and MARION, and evinces certain characters which, to my mind, indicate a more primitive grade of evolution. I refer to the separation throughout their length of the muscle bundles from each branchial arch, and to the fact that all the bundles, with the sole exception of the first, are inserted directly on the coracoid bar.

In Scyllium (fig. 2), then, *c.br.* is a stout columnar muscle which, arising from the

dorsal surface of the coraco-arcual septum, from just behind the fused trunk of the first and second afferent arteries to the level of the third afferent artery, is inserted on the inner border of the first hypobranchial and on the dorsal aspect of the basihyal. The c.br. of either side are in contact in the middle line from a very short distance behind their insertions to their origins on the septum. I agree with VETTER, who observed a similar condition in *Heptanchus*, that the part-insertion of this muscle on the basihyal is a secondary relation, formed in consequence of the diminution of the first hypobranchial, and does not prevent this muscle from being regarded as that of the first gill-arch. C.br. 2, inserted mainly on the second hypobranchial, but by a few fibres also on the second ceratobranchial, runs as a column of muscle to the anterior rim of the coracoid. It is in contact with its fellow of the opposite side, with which it blends to a certain extent, in the region of its origin; dorsally the two divide, allowing passage for the ventral aorta. C.br. 3 and 4 resemble c.br. 2 in origin and insertion, and are found in sequence behind it. They, however, are separated throughout their length from their fellows of the opposite side by the presence in this region of the pericardium. C.br. 5 presents a greater surface to the exterior than any of the foregoing muscles, but is also considerably thinner. It is fairly distinctly divided into three portions, all of which, taking origin on the broad anterior face of the coracoid, opposite the abductor muscles of the fin, are inserted on the inner aspect of the fifth ceratobranchial.

In *Acanthias*, the stout columnar muscle which arises on the most anterior portion of the coraco-arcual septum, and from it runs forwards and upwards, must be regarded as c.br., although its insertion is found to be entirely on the dorsal aspect of the basihyal cartilage. As VETTER maintained, the connection of this muscle with the hyoid arch is almost certainly a secondary condition, consequent upon the extreme reduction of the copula of the first branchial arch; the muscle corresponds in its general topography with the muscle which we have described as c.br., in *Scyllium* and *Heptanchus*. MARION also adopts this nomenclature, and therefore, presumably, this view of the homology of these muscles. C.br. is separated by a strong aponeurosis in the middle line from its fellow of the opposite side.

The remaining coraco-branchiales (c.br. 2-5) form the lateral wall of the pericardium. With the exception of the most posterior one (c.br. 5), they are attached ventrally not to the coracoid, as in *Scyllium*, but to a strong fascia which covers the dorsal face of the c.a.c. and extends laterally to the superficial branchial muscles. In this region they are difficult to distinguish one from another; MARION regards them as a single sheet of muscle. Certainly I have never found them so distinct as is indicated by VETTER in his drawing of *Acanthias* (*op. cit.*, Taf. xv, fig. 8).

C.br. 2 is inserted into the second hypobranchial; c.br. 3 and 4 are inserted mainly on the third and fourth hypobranchials, but to a slight extent also on the corresponding ceratobranchials. C.br. 5 is inserted on the inner aspect of the fifth ceratobranchial and (wherein it differs from the corresponding muscle in *Scyllium*)

on the outer ventral aspect of the basibranchial plate. It shows no sign of division into segments such as we have observed in *Scyllium*.

Turning now to *Rhina*, we again approach new ground, but, with a few trivial exceptions, the characters of the coraco-branchial musculature are readily conformable to type. In accordance with the flattened shape of their possessor, these muscles are more flattened than in the shark-like forms. The arteries pass outwards in the normal manner.

C.br. 1, inserted mainly on the first hypobranchial and in part also on the dorsal aspect of the basihyal, runs backwards almost in the same horizontal plane to its origin on the anterior part of the dorsal aspect of the coraco-arcual septum.

The remaining coraco-branchiales, inserted in turn into the succeeding branchial arches, take origin from the coracoid itself beneath the coraco-arcuales communes. C.br. 2-4 become inextricably fused with one another for a short distance in front of their origins; they then separate to go to their insertions on the appropriate arches. These insertions are, as usual, mainly on the hypobranchials, but there is an increasing tendency to send fibres to the ceratobranchials also as we proceed from before backwards. The hindermost muscle of this series, c.br. 5, is composed of a very broad sheet which is distinctly divided into two portions.

In *Raia* we meet with a very specialised condition of the coraco-branchial muscular system. From its attachment to the angle of pectoral girdle, immediately lateral to the origin of the c.a.e. and contiguous dorsally with the l.p., the muscle runs obliquely inwards, keeping its horizontal plane and showing no signs of dividing into separate bundles. It passes external to the trunk which divides into the third, fourth, and fifth afferent branchial arteries, to its main area of insertion on the anterior process of the basihyal and the membranous floor of the mouth. In the dorso-lateral region it also gives off a few fibres which are attached to the hypo- and ceratobranchials; these are the only vestiges of the c.br. 2-4. Posteriorly there is a strong connection with the fifth ceratobranchial; this represents c.br. 5. I have been unable to detect a trace of c.br. 1.

(iv) Coraco-hyoideus (c.hy.). *Cervicalis profundus* pars, HUMPHRY; *Coraco-hyoideus*, VETTER, WIEDERSHEIM, MARION.

The coraco-hyoideus is usually a massive muscle which extends from the coraco-arcual septum to the basihyal cartilage; its length varies inversely with that of the coraco-arcualis communis. The c.hy. is not as a rule marked by myocommata, though VETTER figures one such division in *Acanthias* and *Heptanchus*.

In *Scyllium*, *Galeus*, and *Acanthias* the c.hy. arises from the ventral face of the coraco-arcual septum. Externally, only its lateral surface can be seen, the median portion being covered by the coraco-mandibularis, to be described later. It runs forwards, in contact with its fellow of the opposite side, and finds insertion on the posterior and postero-dorsal border of the basihyal. Its relative length is greatest in

Galeus, where it extends almost to the coracoid bar, and least in *Acanthias*, where it extends less than three-fifths of the distance between the basihyal and the coracoid.

In *Rhina* this muscle is exceedingly short, but of great strength, and is inserted on the ventral aspect of the ceratohyal as well as upon the basihyal. On the latter it is inserted through the medium of a strong tendon; moreover, the insertion is diagnostic in showing an unpaired median portion, formed by the union in that area with its fellow of the opposite side.

In *Raia* this muscle is very much reduced, probably in correlation with the development of a muscle, the coraco-hyomandibularis, to be described later. I have been able to verify MARION'S observation that, arising from the fascia covering the c.h.m., it is inserted upon the minute hypohyal cartilage.

(v) Coraco-hyomandibularis (c.h.m.). Coraco-hyomandibularis, MARION.

Of the types examined, this muscle occurs only in *Raia*. In that form it is present as a large strip of muscle—the strongest, in fact, of all the ventral muscles—which, arising from the fascia limiting the coraco-arcuales communes as far forward as the fork of the ventral aorta, runs outwards and forwards (passing dorsal to the first hypobranchial) to its insertion on the antero-ventral aspect of the hyomandibular cartilage.

(vi) Coraco-mandibularis (c.m.). Depressor mandibuli, OWEN; Coraco-mandibularis, VETTER, WIEDERSHEIM, TIESING, MARION, etc.

This muscle arises from the coracoid bar in the ventral middle line, or, more frequently, from the coraco-arcual septum; it is the most superficial of the series of muscles under consideration, and, passing forwards in a straight line, becomes inserted on the posterior border of the mandible. The muscle may be either azygous or divisible into two portions; it is not divided by myocommata.

In *Seyllium* and *Galeus* the c.m. is tolerably distinct from its fellow of the opposite side, owing to the presence of a longitudinal septum in the ventral middle line; this is particularly noticeable in the region of insertion on the mandible. In *Acanthias* the c.m. is an azygous muscle. The length of this muscle varies inversely with that of the coraco-arcualis communis; thus, in *Galeus* the muscle is of great relative length, almost touching the coracoid bar, while in *Acanthias* it is relatively short.

In *Rhina* the c.m. is entirely wanting.

In *Raia* the c.m. is a thin strip of muscle, separated by a fascia from its fellow of the opposite side, extending from the mandible direct to the anterior border of the coracoid itself. Right up to its origin on the coracoid it is distinct from the other muscles of the coraco-arcual system.

## 2. PECTORAL FIN.

(1) *Adductor (dorsal or inner) Musculature.*

The adductor muscle of the fin is a fan-shaped structure, composed of a number of muscle bundles which radiate from the axil to the blade. With the exception of a few of the outermost (the first three in *Scyllium*), each bundle is divided horizontally into two portions, so that the whole muscle appears to be divided into two superimposed layers. Most authors recognise but one layer in this muscle. DAVIDOFF (20), who studied very thoroughly the musculature of the pelvic fin of Elasmobranchs, distinctly states that in that region there are two layers in Selachians (*Acanthias*). The evidence which I have been able to collect from the large amount of embryological work published on this subject militates against the view that the division of the muscle into superimposed layers is of real morphological value. BALFOUR's figure of the development of the pectoral fin of *Scyllium* (81, pl. xviii, fig. 7) certainly appears to show two layers in the adductor muscles. This may, however, only be an apparent layering; the "radial muscles" (= adductor bundles) are admittedly oblique in older embryos (such as that figured), and this involves a certain amount of overlapping of adjacent radial muscles; thus, the segments appearing in the section may represent parts of different muscles, not different parts of the same muscle. That two layers exist in the adult, at all events in the proximal region, there can be no doubt; the outer layer is attached to the girdle, the inner to the proximal cartilages of the fin, and between the two a well-marked cavity is found. Proceeding outwards the layers approximate to one another, and finally coalesce so closely that it becomes difficult to separate them. The muscle will be described here in terms of two layers, namely, adductor superficialis (add.s.) and adductor profundus (add.p.).

## (i) Adductor superficialis (add.s.).

Arises from the scapula and is inserted into the adductor profundus. In *Scyllium* the three preaxial bundles are not divided; that is to say, they may be regarded as belonging entirely to the superficial layer, since they arise on the scapula. These three bundles are inserted on the propterygium and propterygial radial. The remainder of the add.s. is divided into two regions, an anterior and a posterior. Near their origins on the scapula the anterior (preaxial) portion passes beneath the posterior, and its innermost fibres become attached to the inner border of the scapula. This arrangement of the superficial muscles allows a certain degree of rotation, or curling, of the fin.

The general arrangement of the superficial layer, with regard to origin and insertion, holds good in all the types under examination; but the division into two overlapping portions is only found in the shark-like forms, while in *Rhina* and *Raja* the muscle bundles radiate in perfectly regular sequence.

## (ii) Adductor profundus (add.p.).

Arises from the proximal cartilages of the fin and is inserted into the distal radials and the horny fin-rays (ceratotrichia). BRAUS (9) maintains that the adductor is inserted only into the horny rays, never into the radials; but my observations do not confirm this statement. The same author has described in great detail the musculature and innervation of the pectoral fin of *Acanthias* (*op. cit.*, Taf. xii, fig. 1), and he shows very clearly the remarkable fact that the muscle bundles correspond neither in number nor position with the distal radial cartilages.

(2) *Abductor (ventral or outer) Musculature.*

The abductor muscle is in most points the counterpart of its antagonist the adductor, though the number of component muscle bundles is not necessarily the same. It may with equal justice be divided into two layers, abductor superficialis (abd.s.) and abductor profundus (abd.p.).

## (i) Abductor superficialis (abd.s.).

Arises from the coracoid and is inserted into the abductor profundus. The first three preaxial bundles, which are inserted on the ventral aspect of the propterygium, show no division into layers, and may be regarded as belonging entirely to the superficial layer; they are best seen from the lateral aspect. The fourth superficial bundle, also lateral in position, has a double insertion, its deepest fibres being inserted into the proximal border of the mesopterygium, while its superficial fibres are inserted into the proximal portion of the propterygial radial and into the fascia covering the first bundle of the abd.p. A similar arrangement will be noted in two of the superficial bundles in *Chimæra*. The first four bundles serve as depressors of the propterygium and its radial. The remaining twenty bundles are visible from the ventral aspect and are inserted in the typical manner.

## (ii) Abductor profundus (abd.p.).

Arises from the metapterygium and is inserted into the distal radials and the ceratotrichia. There is a small muscle which, arising from the outer portion of the mesopterygium, is inserted into the most preaxial horny rays; this must be regarded as the first (preaxial) deep bundle, and corresponds with the fourth bundle of the superficial series. The second bundle of the abductor profundus is inserted into all the remaining ceratotrichia articulating with the propterygial radial.

The above description of the abductor musculature applies to *Scyllium*, and lack of time has rendered impossible anything but a superficial examination of the other types. So far as my observations go, they indicate that the condition of the musculature in *Scyllium* is typical of the general arrangement in *Selachian* fishes.

## II. Holocephali.

*(Chimæra monstrosa, Callorhynchus antarcticus.)*

## 1. SHOULDER GIRDLE.

(1) *The Lateral Muscle.*

The lateral muscle conforms, both in structure and external appearance, to the typical condition in Elasmobranch fishes. This condition has already received sufficient notice in the section on Selachii.

(2) *The Posterior Muscles.*

The parts of the lateral muscle which go to form the retractors of the pectoral girdle in the Holocephali have attained a much higher grade of specialisation than has been encountered among the Selachians. The retractor muscles under consideration are not merely interrupted portions of the segmented lateral muscle, but separate sheets, enclosed in their own fasciæ, and devoid of all trace of myocommata (except in the two lower sections of the mesio-ventral portion). They will be taken in the following order:—

- (a) Retractor dorsalis pectoralis.
- (b) Retractor latero-ventralis pectoralis :
  - (i) Externus.
  - (ii) Internus.
- (c) Retractor mesio-ventralis pectoralis :
  - (i) Superior.
  - (ii) Medius.
  - (iii) Inferior.

(a) *Retractor dorsalis pectoralis (r.d.p.)*.—This is a broad thin sheet of muscle which, arising from the portion of the lateral muscle immediately above the lateral line, runs in a direct, antero-posterior direction to be inserted on the inner aspect of the posterior rim of the scapula and of the backwardly projecting distal horn of that cartilage. In *Chimæra* the muscle is of considerable length, extending to the third myocomma behind the scapular horn, from which myocomma the majority of its fibres take origin. In *Callorhynchus*, on the other hand, the muscle is relatively short, its fibres taking origin from the myocomma which touches the tip of the scapular horn. In both genera the scapular horn extends above the level of the latero-dorsal portion of the lateral muscle; the retractor muscle, therefore, comprises part of the mesio-dorsal portion in addition to the entire latero-dorsal portion; it thus corresponds to the r.m.d.p. and r.l.d.p. of Selachians. As, however, it is not divided longitudinally, it is designated here simply as the r.d.p., or the retractor muscle which is derived from the dorsal moiety of the lateral muscle.

This and the muscle next to be described are figured by VETTER (88, Taf. xii, fig. 1), but erroneously, for they are represented as parts of one and the same muscle sheet, whereas they are in reality divided very distinctly by the lateral line; moreover, their fibres take different directions.

(b) *Retractor latero-ventralis pectoralis (r.l.v.p.)*.—Two straps of muscle (fig. 12) are given off from the latero-ventral portion of the lateral muscle, one of which (externus) is inserted on the outer aspect of the scapula, while the other (internus) is inserted on its inner aspect.

(i) R.l.v.p. externus.

In *Chimæra* this muscle is covered to such an extent by the elevator muscle of the propterygial radial and the r.m.v.p.sup. that it is scarcely visible until the latter are reflected; in *Callorhynchus*, on the other hand, where the first of these muscles is wanting and the second is much more limited in extent, a large tract of the r.l.v.p.ext. in the region of its insertion is visible without dissection. Inserted by a broad tendon in a slight groove on the outer aspect of the scapula, and extending a short distance above the level of the lateral line, the muscle fibres run obliquely, especially in *Callorhynchus*, downwards.

(ii) R.l.v.p. internus.

This muscle lies slightly ventral as well as internal to the foregoing in *Chimæra*, but in *Callorhynchus* is directly beneath it. Taking origin from the latero-ventral mass, its fibres pass, gently downwards in *Chimæra*, parallel to the major body-axis in *Callorhynchus*, to their insertion on the inner aspect of the scapula.

(c) *Retractor mesio-ventralis pectoralis (r.m.v.p.)*.—As in the Selachians, the mesio-ventral portion of the lateral muscle is attached by three tolerably distinct areas of insertion to the girdle; but, except in *Callorhynchus*, it shows no tendency to spread upon the fin muscles. The entire mesio-ventral portion is intercepted at the pectoral girdle.

(i) R.m.v.p. superior.

In *Chimæra* this is an extensive sheet of muscle, whose fibres, arising from the fascia covering the lateral muscle, immediately below the lateral line, run obliquely downwards and forwards to their insertion on the posterior rim of the scapula. The dorsal fibres take origin from the fascia covering the surface of the latero-ventral portion, and for 20 mm. extend as far as the lateral line, this extent beginning 19 mm. behind the scapula; thenceforward the end-line bends downwards, arc-wise, and the ventral fibres gradually fuse with the latero-ventral portion and the middle section of the mesio-ventral portion. It is no longer recognised as a girdle muscle, but as the upper section of the mesio-ventral portion of the lateral muscle. Ventrally, the muscle is separated by a distinct fascia from the r.m.v.p.med.

*Callorhynchus* differs from *Chimæra* in that the r.m.v.p.sup. is continuous ven-

trally with the r.m.v.p.med., in which region also it show traces of myocommata. The latter disappear entirely in the dorsal area of this muscle. The uppermost end-line of the fibres, though arc-shaped, is less convex, and at its nearest point only extends within 19 mm. of the lateral line. In the region of insertion the superficial fibres of this muscle pass clear of the girdle, external to the scapula, to blend with those of the superficial constrictor muscles. This condition recalls that which is described by HUMPHRY for *Mustelus*, and which obtains in numerous other shark-like Selachians; in *Chimæra* this junction does not take place.

(ii) R.m.v.p. medius.

As in Selachians, this muscle is formed by the entire middle section of the mesio-ventral portion of the lateral muscle where it comes in contact with the girdle. The insertion is upon the inner aspect of the posterior rims of the scapula and coracoid from the ventralmost insertion of the r.m.v.p. sup. (and, in *Chimæra*, for some distance above and internal to that insertion) to the ventro-lateral angle of the body-wall. The muscle shows no tendency to spread upon the fin-muscles. The fibres run obliquely upwards from their insertions, and are intercepted a short distance behind the girdle by myocommata.

(iii) R.m.v.p. inferior.

This muscle only appears on the ventral aspect, and its fibres, inserted on the posterior face of the coracoid, run directly backwards parallel to the major body-axis. It is formed by the entire lower section of the mesio-ventral portion of the lateral muscle, which remains undifferentiated right up to its point of insertion.

(3) *The Anterior Muscles.*

In the anterior region we again encounter in the Holocephali an advanced state of evolution of the muscles which work the pectoral girdle. The muscles will be described in the following order, homologies with those of Selachians being implied by the use of identical terms:—

(a) *Protractor dorsalis pectoralis.*

(b) Muscles derived from the mesio-ventral portion of the lateral muscle:

(i) *Levator pectoralis.*

(ii) *Coraco-branchiales.*

(iii) *Coraco-hyoideus.*

(iv) *Coraco-mandibularis.*

(a) *Protractor dorsalis pectoralis (p.d.p.)*—It has already been seen that a large sheet of muscle derived from the entire latero-dorsal portion and to a certain extent from the mesio-dorsal portion of the lateral muscle is inserted on the posterior border of the uppermost section of the scapula; this was designated the retractor dorsalis pectoralis. Another muscle, of precisely similar extent, bestrides the

anterior border of the scapula, and its fibres, passing forwards and slightly downwards, take origin on the posterior aspect of the strong post-orbital ridge of the cranium; to this muscle the name protractor dorsalis pectoralis is given.

The p.d.p. is covered to a certain extent by the l.p.; this is particularly marked in *Callorhynchus*, where a tract of the latter muscle is excised in the drawing in order to expose the insertion of the former.

(b) *Muscles derived from the mesio-ventral portion of the lateral muscle.*

(i) Levator pectoralis (l.p.). Trapezius superficialis, VETTER; Trapezius, JAQUET.

Arising from the post-orbital ridge of the cranium, opposite to the lower half of the orbit in *Chimæra*, opposite the entire orbit and extending above its level in *Callorhynchus*, the fibres of this muscle run backwards and downwards to their insertion on the outer aspect of the scapula. The insertion extends in an arc in *Chimæra*, while in *Callorhynchus* it runs in a straight line, parallel with that of r.l.v.p. The similarity of the insertion levels of the muscle under consideration and of the r.l.v.p., and the similar direction taken by their fibres, led me at first to believe that the former was also a derivative of the latero-ventral portion of the lateral muscle—in fact, that it represented the p.l.v.p. of Selachians. The origin of the muscle high up upon the cranium seemed also to agree with such a conclusion. VETTER's observation that this muscle in *Chimæra* is innervated in a precisely similar manner to the "trapezius" (*i.e.* levator pectoralis) of *Acanthias*, namely, by certain twigs from the ramus intestinalis of the vagus, seems to me a weightier argument than one based on mere topographical grounds. Moreover, there is a small muscle, figured and described by VETTER as trapezius profundus, which lies beneath the foregoing mass. The origins of these muscles are conterminous, they run parallel to one another, but whereas the larger outer one is inserted upon the scapula, the smaller inner one is inserted upon the last pharyngo-branchial. Now, this last recalls the small muscle which was mentioned under the Selachii (see p. 540) as a part of the so-called trapezius. It appears, then, that the protractor latero-ventralis pectoralis is entirely wanting in *Holocephali*.

(ii) Coraco-branchiales (c.br.). Coraco-branchiales, VETTER, JAQUET.

A muscular sheet of uniform thickness, arising from the anterior border of the girdle (both scapular and coracoid portions), is inserted by very short branches on the lowermost portions of the gill arches, thus indicating its composite structure. From the nature of their insertions it follows that the fibres are short dorsally and increase in length as the ventral border of the muscle is approached. The muscle serves, as in the Selachians, to form the lateral wall of the pericardium.

VETTER has described this muscle in considerable detail for *Chimæra* (88, Taf. xii, fig. 5).

The general relations of the muscle are similar in *Callorhynchus*.

The nervous supply is derived from the anterior branch of the united ventral roots of spinal nerves I and II.

(iii) Coraco-hyoideus (c.hy.). Coraco-hyoideus, VETTER, JAQUET.

There is a marked dissimilarity in the two types under consideration in respect of this muscle.

In *Chimæra* it arises from the anterior face of the V-shaped septum described above, its outermost fibres being attached further back and more superficially than the median ones, since the latter are displaced by the origin of the deepest portion of the coraco-mandibularis. The median fibres meet their fellows of the opposite side, but do not fuse with them; from this median line of contact the muscle masses of either side slope downwards and outwards, thus forming the furrow in which runs the keel of the c.m. The insertions of the c.hy. of both sides are contiguous, and occur upon the postero-dorsal aspect of the basihyal cartilage.

There is another muscle mass, which VETTER regarded as the posterior portion of the c.hy., and which must probably be regarded in part, at least, in that light. Arising from the anterior border of the girdle, from just above the origin of the c.m. to the level of the glenoid border (where it is covered by the c.br.), the fibres of this muscle run downwards and slightly outwards to their insertion on the posterior face of the V-shaped septum. Since not only the fibres of the c.hy. are attached to the anterior face of this septum, but also those of the c.m. 2, the muscle may be compared to the coraco-arcualis communis of Selachians. Pending further evidence, I do not propose to alter VETTER's description of the coraco-hyoideus of *Chimæra*.

In *Callorhynchus* the c.hy. is a relatively slender paired muscle which, arising from the dorsal aspect of the c.m., runs forward to its insertion on the basihyal cartilage. There is no manifestation of a posterior portion of the muscle connecting it with the coracoid, such as has been described for *Chimæra*. It is not implied that no fibres of the c.hy. reach the coracoid, but that any such are so completely blended with the huge c.m. that they cannot be distinguished from it. In fact, the neck muscles of *Callorhynchus* have attained a state of fusion which would render comparison with the Selachian type obscure, were it not for the intermediate condition which has been observed in *Chimæra*.

(iv) Coraco-mandibularis (c.m.). Coraco-mandibularis, VETTER, JAQUET.

The coraco-mandibulares of the Holocephali expand anteriorly, and their tendinous insertions cover nearly the entire ventral aspect of the mandible. There is a fairly distinct division of the insertion into an outer, superficial portion (c.m. 1 of VETTER) and a median, deeper portion (c.m. 2 of VETTER). The latter is an azygous muscle, composed of the united median fibres of the c.m. of either side. The central portion is not severed completely from the lateral portions, for the deeper fibres of both portions are in contact; the fascial fold which serves to separate the muscles superficially is sufficiently diagnostic to be of descriptive value.

The fibres from the outer line of insertion (c.m. 1) run inwards, and those of either side eventually meet at a point (35 mm. *Chimæra*, 25 mm. *Callorhynchus*) behind the exposed portion of the mandible, thus hiding the fibres which run from the main line of insertion (c.m. 2) nearly parallel to the long axis of the body. After coalescing, the c.m. portions of either side unite and are only barely distinguishable superficially, while internally their fibres become intermingled. The united c.m. portions gain in depth at the expense of their width, and the depth is further increased by the addition of fibres from the azygous (c.m. 2) portion.

So far the two types under consideration are uniform, but from this point onwards they require separate consideration. In *Chimæra* the main mass of the c.m., derived from the entire c.m. 1 portion and from the superficial fibres of the c.m. 2 portion, is found to take origin from the deep groove on the anterior face of the coracoid symphysis. The remaining fibres of the c.m. 2 portion, shortly behind their insertion, become piled upon one another so as to form a vertical keel of muscle. This keel runs in a deep groove between the coraco-hyoideus muscles, from which it is separated by a fascia. At a point about 45 mm. behind their insertion the fibres which compose the keel are intercepted by a V-shaped septum, whose apex is directed posteriorly. The deepest fibres of the c.m. may thus be described as arising from a wedge-shaped septum between the c.hy. muscles. Through a circular opening in either face of this septum passes the branch of the combined ventral roots of spinal nerves I and II which innervates the deep portion of the c.m. The above account differs from that of VETTER in that the superficial fibres of the c.m. 2 portion are described as running directly from their insertions on the mandible to join the deep fibres of the c.m. 1 portion near their origin, whereas VETTER describes the entire c.m. 2 portion as arising from the septum in question. VETTER, however, remarks that the c.m. 1 portion is augmented in the region of its origin by certain fibres from the septum, and my observations corroborate this. Briefly, the question at stake is: Are all the fibres, which arise from the anterior rim of the coracoid and are inserted on the median (c.m. 2) area of the mandible, intercepted in their course by a septum? VETTER's answer is in the affirmative, mine in the negative. It is perfectly possible that there is variability in this respect, though my observations are drawn from an examination of four adult specimens; but, in any case, the fact remains that the distinction between the two portions of the coraco-mandibularis (c.m. 1 and c.m. 2) is purely superficial. The condition recalls that observed in Rhina among Selachians.

In *Callorhynchus* the c.m. runs without interruption throughout its depth from the mandible to the pectoral girdle; the mass is characterised by its enormous bulk and by the peculiar distribution of its component fibres. The divisions of the c.m. in the area of insertion have been indicated above; the superficial fibres of the c.m. 1 portion, running towards the ventral middle line, soon cover the original ventral superficial fibres of the c.m. 2 portion, while their outer border is defined by a sharp

ridge, above which is a deep trough, gouged, as it were, from the lateral aspect of the muscle. This ridge and trough are most marked anteriorly, and gradually disappear posteriorly, the ridge being rounded off and the trough filled out; this effect is attained at a quarter of the length of the muscle from its origin on the coracoid. The deeper fibres of the c.m. 1. portion, instead of making for the middle line, sweep outwards and upwards, forming the floor of the trough which was mentioned above, and find origin on the anterior face of the girdle. The origin of this portion is, in its ventral area, exposed on the lateral aspect (after removal of the gills and operculum); dorsally, however, it is covered by the coraco-branchiales, beneath which it extends upwards to the scapular region of the girdle, slightly above the level of the adductor muscles of the fin. The c.m. 2 portion is not interrupted, as in *Chimæra*, by a septum, but extends as a solid mass of muscle within the outer coating of the c.m. 1 portion. The mesial fibres of the c.m. 2 portion blend with the mesial fibres of the c.m. 1 portion, where the faces of these muscles are in contact, and accompany them to their origin. The lateral fibres sweep outwards and upwards, running beneath and parallel to the lateral fibres of the c.m. 1 portion. This powerful mass of muscle, which represents the fused coraco-mandibulares of either side, is, then, near its origin on the pectoral girdle, a homogeneous structure, whose section is U-shaped, the concavity being directed dorsally.

## 2. PECTORAL FIN.

The morphology of the pectoral fin skeleton of the *Chimæroids* has been discussed by HOWES (48, p. 22). In this discussion, MIVART'S interpretation of the relationship of the parts is advocated, and subsequent authors (e.g. GOODRICH, *Lankester's Treatise Zool.*, ix, p. 81, *Callorhynchus*) appear to accept this view. The fin is supported upon two basal elements, both of which articulate with the glenoid border of the pectoral girdle; the postaxial is held to represent the metapterygium, the preaxial the propterygium (the mesopterygium is wanting). A diagnostic triangular cartilage, whose base articulates proximally with the propterygium, represents the fused portions of the four propterygial radiales; this will be designated in brief the propterygial radial.

### (1) *Adductor Musculature.*

The adductor musculature closely resembles that of Sharks; that is to say, a series of muscle-bundles radiate fanwise from the coraco-scapular region of the girdle to the blade of the fin. The two preaxial bundles, inserted on the propterygium and propterygial radial respectively, are specialised and will receive separate treatment. The remaining thirty-one bundles are divided, though indistinctly as in *Selachians*, into a superficial and a deep layer. DAVIDOFF (20) recognises a layering in the adductor musculature of the pelvic fin of *Chimæra*.

The following account is based on a study of *Chimæra* alone, a certain striking point of difference from *Callorhynchus* being noted in passing.

## (i) Adductor superficialis (add.s.).

The main mass of this muscle arises on the outer border of the scapula and is inserted into the underlying adductor profundus. The first two adductor bundles (preaxial) are not divided into layers and may be described, as in Selachians, as belonging entirely to the superficial series. The first, arising from the postero-external border of the scapula, opposite to the upper third of the coraco-branchialis, runs downwards and slightly outwards to its insertion on the inner upper border of the propterygium; as it fills the axil of the fin its shape conforms approximately to that of a wedge. The second in *Callorhynchus* follows a parallel course and finds insertion on the propterygial radial; but in *Chimæra* we meet with a very striking modification. The insertion is strap-like, partly tendinous, and occurs on the proximal fifth only of the propterygial radial; from here the fibres run almost vertically to take origin not only from the outer surface of the scapula (opposite to the insertion of the l.p.), but also from the fascia covering the r.l.v.p. as far up as the lateral line. (See fig. 6.)

The third superficial bundle has a distinct origin in the cavity of the scapula near the preaxial end of the glenoid border; it is very slender and soon fuses with the much stouter first bundle of the deep series, which in turn is inserted into the distal portion of the propterygial radial. The remaining thirty bundles are divided into two groups, of which the preaxial, as in Selachians, is overlapped near its origin by the postaxial. The preaxial group consists of twenty-one bundles in the example figured; these arise from a bowl-like cavity in the coraco-scapular region of the girdle opposite to the middle of the glenoid border. The bundles are by no means distinct in the region of origin, and the muscle is characterised by the great depth in comparison to its width. As the fibres pass outwards they spread laterally, and, as a consequence, the mass becomes shallower. They begin now to be collected into bundles, which become more and more distinct as the distal extremity of the muscle is reached. The deepest fibres, when they reach the level of the basal cartilages of the fin, blend with the underlying adductor profundus. In fig. 10 the superficial bundles appear to be inserted entirely at the distal extremity of the corresponding deep bundles; it should be pointed out that this is a diagrammatic representation, the remainder of the insertion (extending almost the whole length of the add.p.) being omitted for the sake of clearness. The remaining nine bundles comprise the postaxial group. These arise from the outer border of the scapula, a short distance above the origin of the preaxial group, and in their outward passage obscure the latter.

## (ii) Adductor profundus (add.p.).

This muscle is composed of bundles which correspond in number and relative position to those of the superficial series described above, with the exception of the two preaxial ones, which, as already stated, have no representatives in the lower

series. There are, then, thirty-one bundles, of which the first takes origin from the superior face of the propterygium and is inserted into the propterygial radial.

(2) *Abductor Musculature.*

The abductor musculature is in the form of a fan-shaped mass which radiates from a considerable area of the coracoid, and, to a slight extent, from the coraco-scapular region, to the outer surface of the fin. The muscle mass is exceedingly dense ventrally; the insertion here extends from the anterior border of the coracoid right round to the posterior border, where it lies parallel with the ventralmost bundle of the adductor series. The result of this formation is that the postaxialmost adductor fibres (fig. 10) actually act as abductors; so that, when the muscle as a whole contracts, the lower (postaxial) border of the fin is curled inwards, while the upper and middle portions are drawn outwards. Moreover, the obliquity of the muscle, owing to the relative lowness of its origin, tends to draw the whole fin somewhat downwards. From the foregoing description of the adductor musculature it is apparent that the action of the latter is to rotate the fin back into its position of rest at the side of the body; this upward and backward sweep of the fin must be largely assisted by the strongly developed second adductor bundle.

(i) *Abductor superficialis (abd.s.).*

The muscle takes origin dorsally from the antero-lateral face of the girdle in the coraco-scapular region, rather below the upper level of the glenoid border; as it is traced ventrally the origin increases in depth, and finally spreads round the lower edge of the glenoid border and upon the posterior face of the coracoid (see fig. 10). The first two (preaxial) bundles are not divided into layers (see fig. 11), and are inserted into the propterygium and propterygial radial. The succeeding two bundles give their deepest fibres to the metapterygium, the more superficial fibres terminating on the propterygial radial and in the corresponding bundles of the profundus system. The bundles thenceforward become less and less distinct.

(ii) *Abductor profundus (abd.p.).*

This muscle takes origin from the metapterygium and metapterygial radials, and is inserted proximally into the palisade-like radials and distally into the actinotrichia. The muscle bundles are very distinct, and, unlike those of the adductor system, run parallel with the palisade cartilages.

### III. Chondrostei.

(*Accipenser rubicundus*.)

#### 1. SHOULDER GIRDLE.

##### (1) *The Lateral Muscle.*

The composition of the lateral muscle of *Accipenser* closely resembles that of the Teleostei, consisting, namely, of four series of hollow cones, two above and two below the lateral line. In the pectoral region four areas can still be traced; of these, the two dorsal are completely severed from the two ventral by the passage of the horizontal septum which runs from beneath the lateral line to the transverse processes of the vertebræ.

The dorsal moiety takes a double origin from the skull. The dorsalmost portion arises from the occiput just below the first dorsal spine and is formed by the upper halves of the dorsal backwardly directed cones, while the ventralmost arises from the exoccipital region and is formed by the ventral forwardly directed cones. This differs from the condition figured by KNAUER for *A. sturio*, in which there appears to be only one area of origin for the dorsal moiety of the lateral muscle.

The ventral moiety is very clearly divided into a latero-ventral and a mesio-ventral portion, which condition also appears in KNAUER's figure of *A. sturio*. In the former the fibres run parallel to the long axis of the body. This is also true for the mid-ventral fibres of the mesio-ventral portion; but as the sides are reached the fibres become increasingly inclined, so that they make an acute angle with those of the latero-ventral portion. The slope of the fibres is from below anteriorly to above posteriorly.

##### (2) *The Posterior Muscles.*

When the lateral muscle reaches the pectoral girdle it becomes inserted to a large extent into the various parts of that structure. The muscles which are attached in this manner act as retractors of the girdle, and will be described in relation to the areas of the lateral muscle from which they are derived.

(a) *Retractor latero-dorsalis pectoralis (r.l.d.p.)*.—Some of the superficial fibres break away from the main mass of the latero-dorsal portion of the lateral muscle and become inserted into the posterior border of the cartilaginous suprascapula.

(b) *Retractor latero-ventralis pectoralis (r.l.v.p.)*.—The entire latero-ventral portion on reaching the girdle becomes inserted into the posterior face of the coraco-scapular cartilage. Not a fibre reaches the cleithrum. The muscle is seen in fig. 15.

(c) *Retractor mesio-ventralis pectoralis (r.m.v.p.)*.—In the Sturgeon this muscle is divided into two portions; the third or "medius" portion figured and described in *Elasmobranchii and Teleostei* is not apparent.

## (i) Superior (see fig. 15).

The markedly oblique fibres which compose the lower part of the lateral body-wall pass into a tendinous sheet which is inserted into the lowermost part of the posterior face of the coraco-scapula.

## (ii) Inferior (see fig. 14).

The ventral body-wall near its middle line passes anteriorly into a sheet of connective tissue which is inserted into the hinder border of the clavicles, forming the ventral wall of the pericardium. Laterally some of the fibres pass forwards, between the pericardial fascia and the coraco-scapula, and internal to the ventrally projecting process of the latter, to be inserted on the bases of the visceral arches. The last-named muscle mass will be described later under the heading claviculo-hyoideus.

(3) *The Anterior Muscles.*

*A. Connections with the Skull.*—The presence of a “trapezius” muscle is denied by GEGENBAUR and VETTER for *Accipenser sturio*. MEISSNER (63) describes such a muscle in *A. nudiventris*, *A. stellatus*, *A. stenorhynchus*, and *Pseudoscaphirhynchus Kaufmani*, and associates its presence with the increased mobility of the shoulder girdle in these forms compared with that in *A. sturio*; he even proposes on these grounds to reinstate the old generic name of *Sturio* for the latter species. OSTROUMOFF describes the development of a “trapezius” in *A. güldenstädtii* and *A. ruthenus*. I have shown the muscles of this area in *A. rubicundus* in fig. 15. It is also present in *Polydon*.

OSTROUMOFF states that the development of the “trapezius” muscle, likewise its innervation (from the ramus accessorius of the vagus), leads to the conclusion that this muscle belongs to the dorsal suprabranchial section of the superficial constrictor, which is not severed into myomeres, and in the beginning of its development includes six myomeres representing the five gill pouches and the sixth rudimentary pouch. Its development pulls the shoulder girdle forwards against the gill apparatus. Thus the embryonic condition in the Chondrostei recalls vividly the adult condition in the Selachii.

MEISSNER also shows that the trapezius is divided into two distinct portions, but does not name them.

## (a i) Protractor pectoralis anterior. Trapezius (pars), MEISSNER.

Lies immediately beneath the skin. It takes origin on the skull just behind the retractor hyomandibularis, and is inserted on the scapula and in part also on the cleithrum.

## (a ii) Protractor pectoralis posterior. Trapezius (pars), MEISSNER.

A very small muscle, lying somewhat deeper and posterior to the foregoing, takes origin on the suprascapula and is inserted on the scapula.

(b i) Levator pectoralis is wanting in the Sturgeon.

*B. Connections with the Visceral Arches.*—In further correlation with the relative immobility of the shoulder girdle, these muscles are fewer in number and smaller in extent than in other groups of fishes.

(b ii) Cleithro-branchialis.\*

This is a compact, strap-like muscle which, inserted on the base of the fifth branchial arch, runs outwards and downwards, spreading slightly fan-wise to its origin on the inner aspect of the lower third of the cleithrum.

(b iii) Claviculo-hyoideus. Coraco-arcualis posterior, VETTER, OSTROUMOFF.

This muscle arises from the ventral anterior border of the clavicle and is inserted at the base of the hyoid arch. Unlike the condition in most Elasmobranchs, this muscle is not divided by myocommata; according to OSTROUMOFF, it is formed by a ventral outgrowth of the third myotome.

The very minute branchio-mandibularis (fig. 14, Br.mn.) of *A. rubicundus* appears to be a vestige of the coraco-mandibularis so characteristic of Elasmobranchs.

## 2. THE PECTORAL FIN.

The details of the fin musculature have not been worked out, but the general composition is diagnostic. Both the adductor and abductor muscles are divided into two layers, a superficialis and a profundus. The fibres of each of these muscles are collected into distinct bundles for insertion on the fin rays.

DAVIDOFF (20) found a similar condition in the pelvic fin of *A. ruthenus*, except that the abductor was not divisible into two superimposed layers.

## IV. Teleostei.

(See List of Types, p. 532.)

### 1. SHOULDER GIRDLE.

#### (1) *The Lateral Muscle.*

A considerable time was devoted to the study of this muscle, and the results are recorded in the *Proceedings of the Zoological Society of London*, "On the Nature of the Lateral Muscle in Teleostei," 1914, p. 319.

#### (2) *The Posterior Muscles.*

(a) *Retractor latero-dorsalis pectoralis.* Retractor scapulæ, OWEN.—The latero-dorsal portion of the lateral muscle is inserted at its anterior extremity on the side

\* It is interesting to note that the Cleithro-branchialis is single in Accipenser, while in Polypterus it is divided into three distinct parts (fig. 24). Both these types differ in respect of this muscle from the condition which is so constant throughout the Teleostei.



of the skull (exoccipital, otic recess, and post-temporal). In some Teleosteans a small superficial branch of this muscle is attached to the supraclavicle (*Blennius pholis*), or to the cleithrum (*Cottus scorpio*), where it is inserted on the posterior border of the backwardly directed spine in which that bone ends.

In *Periophthalmus* the mesio-dorsal portion of the lateral muscle gives a small branch to the upper border of the post-temporal; but this is exceptional in the Teleostei.

Where this muscle is present the r.l.v.p., next to be described, is wanting, and *vice versa*.

(b) *Retractor latero-ventralis pectoralis*. Retractor scapulæ, OWEN.—M'URRICH (60) states that the latero-ventral portion of the lateral muscle (his third portion) disappears in *Amiurus* before reaching the shoulder girdle; such is the case in some other Teleosteans, but in the majority a small bundle of fibres, undoubtedly belonging to this portion, is attached to the upper extremity of the cleithrum, or to the supraclavicle (*Trigla gurnardus*), or to both (*Lophius piscatorius*). The muscle is frequently flat and fan-shaped.

In *Lophius* this muscle has undergone most remarkable modifications, probably in accordance with the extraordinary mobility of the limbs in that form. HAMBURGER (42) has already given an account of the musculature of the fore limb of *Lophius*; but, as his description is incomplete, and he has neither named nor illustrated the individual muscles, and as the case is of peculiar interest, I shall deal with it here in detail. Fig. 22 shows the dorsal aspect of the right shoulder after removal of the skin, the latero-dorsal portion of the lateral muscle, and the retractor mesio-ventralis pectoralis superior: the various parts of the r.l.v.p. are numbered i-v.

Part i is a strap-like muscle inserted mainly on the ventral surface of the supraclavicle, but in part also on the dorsalmost extremity of the cleithrum (ventral aspect).

Part ii is a strap-like muscle inserted on the dorsalmost portion of the cleithrum above the origin of i. It is also distinguished by its darker colour.

Part iii is a flattened cylindrical mass inserted in a slight hollow on the ventral aspect of the cleithrum immediately behind the glenoid border. It passes inwards and downwards, between parts ii and v, so as to cover the peritoneum.

Part iv is a strap-like muscle given off by part v at a level defined by producing the long axis of the supraclavicle, and inserted into part iii at a level slightly adaxial to the backwardly directed process of the cleithrum.

Part v is a powerful strap of muscle inserted on the ventral aspect of the abaxial third of the horizontal stem of the cleithrum. It curves abruptly inwards and then upwards.

Parts i, ii, and v do not go to form part of the latero-ventral body muscle, but take origin by a fascia along the lateral line. It might be supposed that these muscles belonged to the latero-dorsal portion, but the fact that part v is blended with part iii (undoubtedly ventro-lateral) through the medium of part iv, indicates

that part v certainly, and parts i and ii probably, should be regarded as derivatives of the latero-ventral portion. Embryological evidence would be of interest here, as in other problems connected with Lophius.

(c) *Retractor mesio-ventralis pectoralis*.—The latero-ventral portion has been seen to decrease in width as it approaches the anterior end, and in some cases completely to disappear. With this decrease of the latero-ventral, the mesio-ventral portion increases in proportion, so that it becomes attached to almost the whole length of the cleithrum. It is divided into two distinct portions, the superior (i) and the inferior (iii), while the medius (ii) portion, axillary, so constant in Elasmobranchs, is vestigial.

(i) R.m.v.p. superior. Subcoracoideus, OWEN; Lateralis 4 (pars), M'MURRICH.

A broad thin sheet of muscle, usually traversed by myocommata, inserted along the posterior border of the cleithrum and, in part, on the coracoid. The insertion is entirely dorsal to that of the fin muscles, and extends nearly to the dorsal end of the cleithrum. In this muscle the post-clavicle, when present, is embedded.

(ii) R.m.v.p. medius.

There is a triangle of connective tissue immediately behind the pectoral fin, and this is traversed by a few muscle fibres, which are inserted on the adductor muscle of the fin. These fibres are the only trace of a "medius" in most Teleostei, but in *Trigla* (fig. 21) the muscle shows considerable development.

(iii) R.m.v.p. inferior. Protractor ischii, OWEN; Lateralis 5, M'MURRICH; Pelvico-clavicularis, HAMBURGER.

This muscle is attached to the cleithrum from just below the fin muscles to the ventral symphysis, where it meets its fellow of the opposite side, with which it is continuous. In those forms whose pelvic fins are thoracic or jugular in position this muscle becomes considerably specialised, and ceases to show the myocommata which are characteristic in lower types; it may then be described as a pelvico-cleithrale (fig. 21).

### (3) *The Anterior Muscles.*

#### A. *Connections with the Skull.*

(a) Protractor pectoralis, LAMBEAU, CUVIER; Protractor scapulæ, OWEN; Occipito-clavicularis, VOGT and YUNG, HAMBURGER; Trapezius, HUMPHRY, M'MURRICH.

This muscle is constantly present in Teleosteans. It takes the form of a fan-shaped mass which, arising from the otic region of the skull, becomes inserted partly into the forward border of the supraclavicle and partly into the cleithrum. The muscle is superficial in position, and forms the posterior border of the upper portion of the gill cavity.

The protractor pectoralis is invariably divided into two distinct portions, as described below.

(i) P.p. anterior.

This part of the muscle is usually slightly internal to the succeeding part. In point of size it may be larger, as in *Zeus faber* (fig. 16), or smaller, as in *Lophius piscatorius* (fig. 22), than the succeeding portion. The insertion is entirely upon the cleithrum, but may take place upon the inner aspect (*Zeus*), or upon the outer aspect (*Lophius*).

(ii) P.p. posterior.

This part of the muscle arises behind the former and is inserted partly upon the supraclavicle, and, to a greater or less extent, upon the cleithrum.

(b i) Levator pectoralis. Diaphragmamuskel, CUVIER; Trapézoïde, VOGT and YUNG; Levator, HAMBURGER; Sternocleido-mastoïdeus, HUMPHRY.

A flattened columnar muscle underlies the foregoing muscles. It arises from the basioccipital or parasphenoid and is inserted on the inner aspect of the cleithrum. This muscle usually forms the lateral wall of the pericardium, and for that reason was named by CUVIER "diaphragmamuskel."

It should be recalled that this muscle is absent in the Sturgeon; in many Teleosteans it is exceedingly minute, and in *Motella* it is absent, unless it is represented in that form by the ligament (figs. 19, 20) which runs from the inner aspect of the cleithrum to the basioccipital. I am inclined to believe that this is not the case, for both in *Trigla* and *Lophius*, which possess a normal levator pectoralis, the ligament is present in addition. It is curious that in *Lophius* this ligament, instead of being inserted on the side of the basioccipital or of the vertebral centra (as in the majority of Teleosteans), unites with its fellow of the opposite side in the space between the kidney and the vertebral column.

B. *Connections with the Visceral Arches.*

(b ii) Cleithro - branchialis. Branchiretractors, OWEN; Pharyngo-clavicularis, VOGT and YUNG, M'MURRICH; Branchio-clavicularis, HAMBURGER.

Two compact little bands of muscle invariably run from the anterior border of the cleithrum to the fourth ceratobranchial. The two muscles run approximately at right angles to one another, and their insertions on the ceratobranchial are usually close together, or even contiguous (*Zeus*).

a. Cl. br. externus.

This muscle arises from the lower third of the cleithrum, and follows an approximately vertical course (*Zeus*, fig. 16). In *Motella* (fig. 20) the muscle runs obliquely upwards. In *Trigla* the muscle is traversed by two transverse septa.

*β.* Cli. br. internus.

This muscle arises, often through the medium of a tendon (Trigla, Zeus, fig. 16), from the upper third of the cleithrum and follows an approximately horizontal course. It is usually considerably broader than the cli.br.ext. HAMBURGER states that in Lophius this muscle is inserted upon the hyo-branchialis muscle, but my dissections do not bear this out; I find that the insertion occurs upon the fourth ceratobranchial in the normal manner; the roots of the two muscles in question are, however, contiguous.

(*b* iii). Cleithro-hyoideus. Sternohyoid, STANNIUS, VOGT and YUNG; Retractor hyoidei, OWEN; Hyo-pectoralis, M'MURRICH; Hyo-clavicularis, HAMBURGER.

A powerful muscle which forms the ventral border of the gill cavity. It has a double origin on the cleithrum; the larger portion arises from the outer aspect of the cleithrum, usually in its lower third, while a smaller portion arises from the region of the clavicular symphysis, where it comes in contact with its fellow of the opposite side. The insertion occurs upon the base of the hyoid arch. The muscle is usually much reduced in bulk as it reaches the point of insertion, but Zeus (fig. 16) forms an exception.

## 2. PECTORAL FIN.

(1) *Adductor.*

The adductor system, as in the foregoing groups of fishes, is divided into two layers—an outer, superficialis, and an inner, profundus. Each of these is divided distally into very distinct bundles which become inserted, usually by long tendons, upon the bases of the lepidotrichia. There is in addition in certain Teleosteans (Zeus, fig. 16) a third, deeper and more ventral, layer, which serves to dilate the fin. The third layer has been described by CUVIER, VOGT and YUNG, and others, and is named the dilator posterior. These muscles take origin in part from the cleithrum and in part from the fin skeleton proper (coracoid, scapula, and radials).

(2) *Abductor.*

The abductor system conforms closely to the adductor in any given type of Teleostean. The third layer, when present, is named the dilator anterior.

(3) *Modifications.*

Extraordinary specialisation of the fin muscles occurs in forms whose pectoral fins have become modified for progression on a solid surface. These modifications have been fully described for Trigla by WILLIAMSON (92).

The most interesting development of the muscles of the pectoral fin in the Teleostei is exhibited by Lophius. HAMBURGER (42) has given a complete account

of this musculature ; but, through some mischance, the descriptions of his drawings are so inaccurate that they would be very difficult to follow without the corrections which I have ventured to make.

The description of figs. 19, 20 is correct ; but in HAMBURGER'S "Figurenerklärung" the descriptions of these two drawings are inverted.

On comparing fig. 17 with the statement in the text no agreement is found. The one muscle shown is marked M.b.r. 1, which the summarised description of this figure tells us is the basi-radialis *internus* ; moreover, that muscle takes origin on a bone denoted Bs. II. Examination of my own material shows that fig. 17 represents faithfully the basi-radiale *internus*—the distal portion of the adductor profundus ; it is thus a view of the dorsal (inner) aspect, not of the ventral as stated. The lettering of the radials (basalia) has been inverted in this particular figure, which accounts for the second discrepancy.

The two muscles described as lying on the inner aspect of the fin in reality form the distal portion of the deeper abductor, or outer system, and are situated as shown in fig. 18. Here the text agrees with the summarised description, but both are at variance with fact.

HAMBURGER divides the fin muscles, for practical purposes, into three systems based on their origins and insertions, but adds that they are divisible also, as in other Teleosteans, into an external and an internal system. The complicated condition of the fin musculature is fairly clearly derivable from the primary Teleostean condition ; they may be classified as follows :—

ADDUCTOR (internal) SYSTEM.	ABDUCTOR (external) SYSTEM.
I. Superficialis.	I. Superficialis.
1. Claviculo-radiale <i>internus</i> .	5. Claviculo-radiale <i>externus</i> .
2. Basi-claviculare <i>internus</i> superf.	6. Basi-claviculare <i>ext.</i> superf. i.
	7. Basi-claviculare <i>ext.</i> superf. ii.
II. Profundus.	II. Profundus.
3. Basi-claviculare <i>int.</i> prof.	8. Basi-claviculare <i>ext.</i> prof.
4. Basi-radiale <i>internus</i> .	9. Basi-claviculare <i>transversus</i> .
	10. Basi-radiale <i>transversus</i> .
	11. Opponens.

To avoid confusion, HAMBURGER'S nomenclature has been retained ; though it must be remembered that here "basi" implies connection with the radials, and "radiale" with the fin rays or lepidotrichia, while references to the "clavicle" are better stated in terms of the cleithrum.

A fold of the preaxial radial grips and covers slightly superficially the claviculo-radiale *internus*, but this is not indicated in HAMBURGER'S illustration (fig. 16). The basi-claviculare *internus* superficialis, as HAMBURGER states, serves to extend the

KEY TO COMPARATIVE STUDY OF PECTORAL MUSCULATURE.

	1. SELACHII.	2. HOLOCEPHALI.	3. DIPSOLO- HUMPHRY (52).	4. CHONDROSTEL.	5. POLYPTERINI.	6. TELEOSTEL.	URODELA. (Similar mus- cles for comparison.)
Posterior fixation muscles.	(a) Retr. lat.-dors. pect. (b) R. lat.-vent. pect. (i) Externus. (ii) Internus. (c) R. mes.-vent. pect. (i) Superior. (ii) Medius. (iii) Inferior.	(a) Retr. dors. pect. (b) R. lat.-vent. pect. (i) Externus. (ii) Internus. (c) R. mes.-vent. pect. (i) Superior. (ii) Medius. (iii) Inferior.	...	(a) Retr. lat.-dors. pect. (b) R. lat.-vent. pect. (c) R. mes.-vent. pect. (i) Superior. (ii) Inferior.	(a) Retr. lat.-dors. pect. (b) R. lat.-vent. pect. (c) R. mes.-vent. pect. (i) Superior. (ii) Medius. (iii) Inferior.	(a) Retr. lat.-dors. pect. (b) R. lat.-vent. pect. (c) R. mes.-vent. pect. (i) Superior. (ii) Medius. (iii) Inferior.	Serratus.  Latiss. dors. Obliquus. Rectus abd.
	(a) Protr. lat.-dors. pect. (b) P. lat.-vent. pect.	(a) Protr. dors. pect. ...	Trapezius.	(a) Protr. pect. (i) Anterior. (ii) Posterior.	(a) Protr. pect. (i) Anterior. (ii) Posterior (?).	(a) Protr. pect. (i) Anterior. (ii) Superior.	Trapezius.
	(c) Meso-vent. dentis. (i) Levator pect. (ii) Coraco-arc. comm. (iii) Coraco-branch. (5 to successive arches). (iv) Coraco-hyoideus. (v) Coraco-hy-mandib. (vi) Coraco-mandib.	(b) (i) Levator pect. (ii) Coraco-branch. (5 to successive arches). (iii) Coraco-hyoideus. (iv) Coraco-mandib.	Stern.-cleido- mast.	(b) (i) Wanting.	(ii) Cleithro-branch. (1 to posterior arch). (iii) Claviculo-hyoid. (Branchio-mandib.)	(ii) Cleithro-branch. (3 to posterior arch). (iii) Cleithro-hyoid.	(ii) Cleithro-branch. (2 to posterior arch). (iii) Cleithro-hyoid.
Anterior fixation muscles.	(a) Adductor. (i) Superficialis. (ii) Profundus.	(a) Adductor. (i) Superficialis. (ii) Profundus.	?	(a) Adductor. (i) Superficialis. (ii) Profundus.	?	(a) Adductor. (i) Superficialis. (ii) Profundus. Dilator posterior (when present).	
	(b) Abductor. (i) Superficialis. (ii) Profundus.	(b) Abductor. (i) Superficialis. (ii) Profundus.	?	(b) Abductor. (i) Superficialis. (ii) Profundus.	?	(b) Abductor. (i) Superficialis. (ii) Profundus. Dilator anterior (when present).	
Fin muscles.							

limb; it is not thus functionally an adductor, though, from its origin on the dorsal aspect of the cleithrum, it should probably be regarded morphologically as a part of the adductor system. The claviculo-radiale externus does not supply the posterior rays, HAMBURGER'S "opposable portion" of the fin. So far I agree, but it is surely a slip which leads him to say that this muscle draws the fin rays upwards, while the claviculo-radiale internus draws them downwards.

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## INDEX TO FIGURES.

## I. CARTILAGES AND BONES.

<i>Br.c.</i> 1-5 = Ceratobranchials 1st to 5th.	<i>Mpt.</i> = Metapterygium.
<i>Br.hyp.</i> = Hypobranchial.	<i>Ppt.</i> = Propterygium.
<i>Cla.</i> = Clavicle.	<i>Ppt.r.</i> = Propterygial radial.
<i>Cli.</i> = Cleithrum.	<i>Pt.cla.</i> = Post-clavicle.
<i>Cor.</i> = Coracoid.	<i>Pt.t.</i> = Post-temporal.
<i>F.r.</i> = Fin ray.	<i>S.cla.</i> = Supra-clavicle.
<i>Hy.b.</i> = Basihyal.	<i>S.sc.</i> = Supra-scapula.
<i>Hy.c.</i> = Ceratohyal.	<i>Sc.</i> = Scapula.
<i>Mn.</i> = Mandible.	

## II. MUSCLES.

<i>Abd.sup.</i>	= Abductor superficialis (Nos. = muscle-bundles, 1 preaxial)
<i>Abd.prof.</i>	= Abductor profundus do. do. do.
<i>Add.sup.</i>	= Abductor superficialis do. do. do.
<i>Add.prof.</i>	= Adductor profundus do. do. do.
<i>Br.mn.</i>	= Branchio-mandibularis.
<i>C.a.c.</i>	= Coraco-arcualis communis.
<i>C.a.s.</i>	= Coraco-arcual septum.
<i>C.br. 1 to 5</i>	= Coraco-branchiales of 1st to 5th branchial arches.
<i>C.hy.</i>	= Coraco-hyoideus.
<i>C.m.</i>	= Coraco-mandibularis.
<i>Cla.hy.</i>	= Claviculo-hyoideus.
<i>Cli.br.ext.</i>	= Cleithro-branchialis externus.
<i>Cli.br.int.</i>	= Do. internus.
<i>Cli.br.ter.</i>	= Do. tertius.
<i>Cli.hy.</i>	= Cleithro-hyoideus.
<i>Dil.a.</i>	= Dilator anterior.
<i>Dil.p.</i>	= Dilator posterior.
<i>L.p.</i>	= Levator pectoralis.
<i>P.cli.</i>	= Pelvico-cleithrale = R.m.v.p.inf.
<i>P.d.p.</i>	= Protractor dorsalis pectoralis.
<i>P.p.ant.</i>	= Protractor (latero-ventralis) pectoralis anterior.
<i>P.p.post.</i>	= Do. do. do. posterior.
<i>R.d.p.</i>	= Retractor dorsalis pectoralis.
<i>R.l.v.p.ext.</i>	= Retractor latero-ventralis pectoralis externus.
<i>R.l.v.p.int.</i>	= Do. do. do. internus.
<i>R.m.v.p.sup.</i>	= Retractor medio-ventralis pectoralis superior.
<i>R.m.v.p.med.</i>	= Do. do. do. medius.
<i>R.m.v.p.inf.</i>	= Do. do. do. inferior.
<i>Ins.</i>	= Insertion of.
<i>Or.</i>	= Origin of.



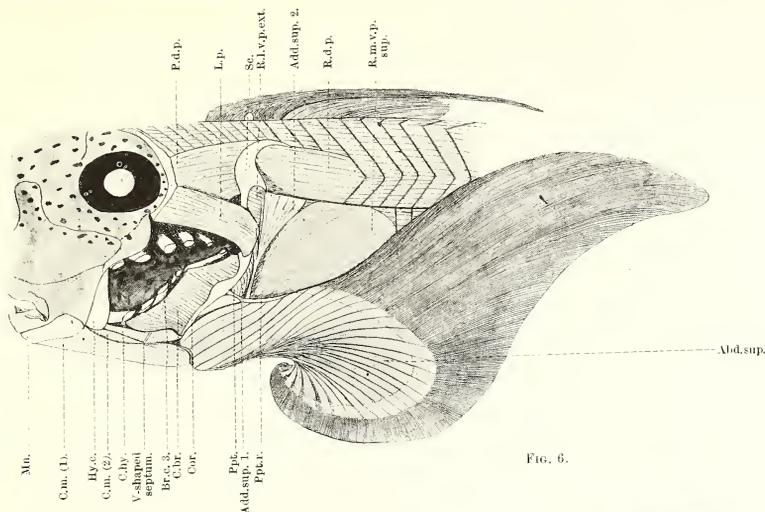


FIG. 6.

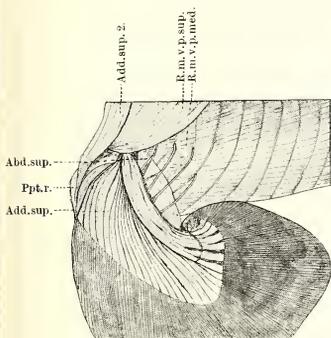


FIG. 7.

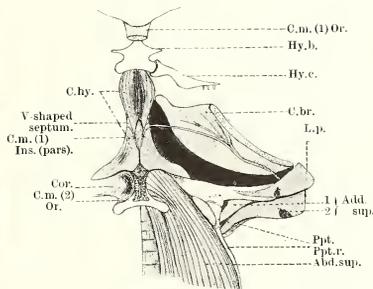


FIG. 9.

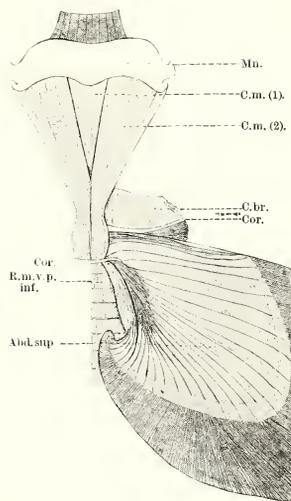


FIG. 8.

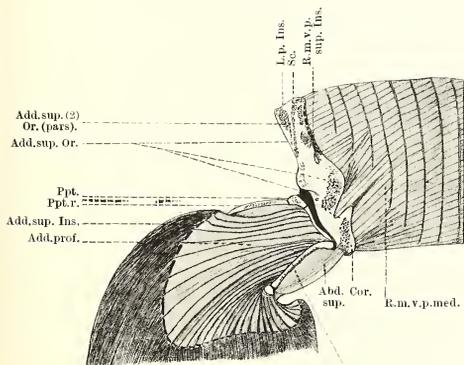


FIG. 10.

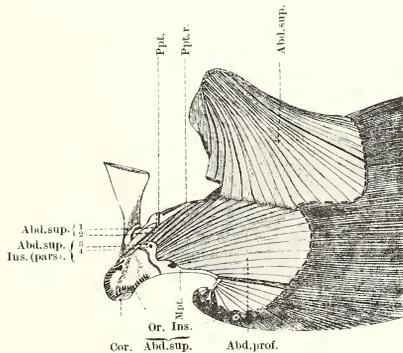


FIG. 11.



Captain E. W. SHANN on "The Comparative Myology of the Shoulder Girdle and Pectoral Fin of Fishes."—PLATE III.

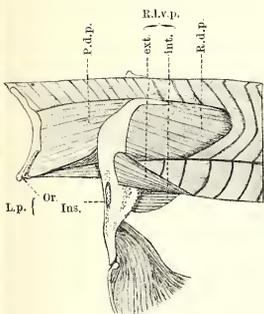


FIG. 12.

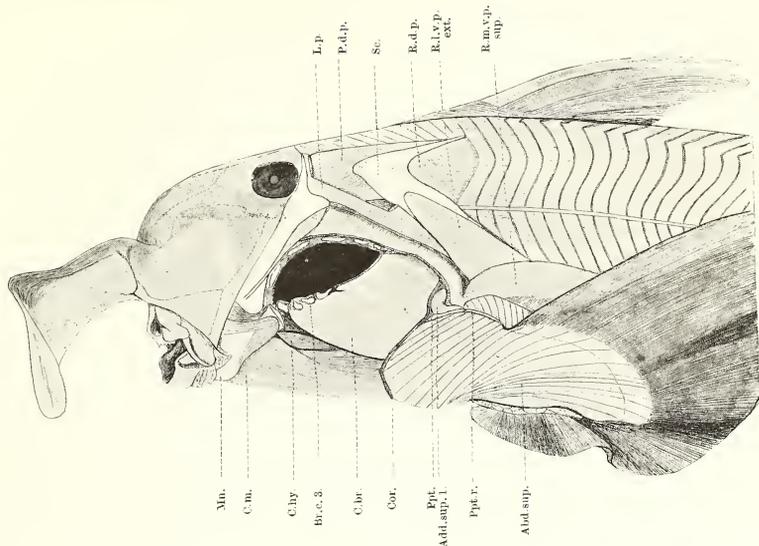


FIG. 13.

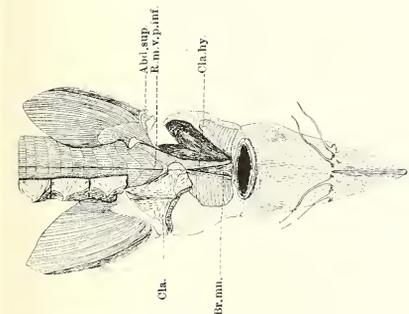


FIG. 14.

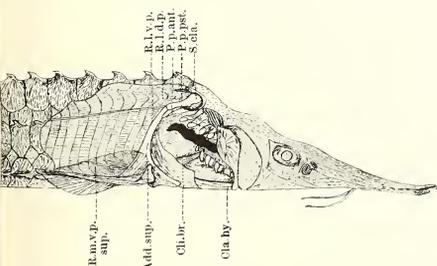


FIG. 15.

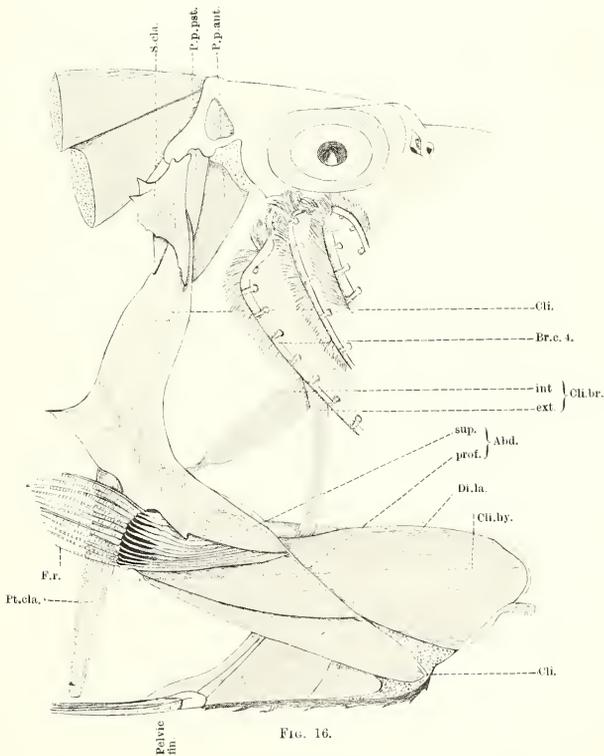


FIG. 16.



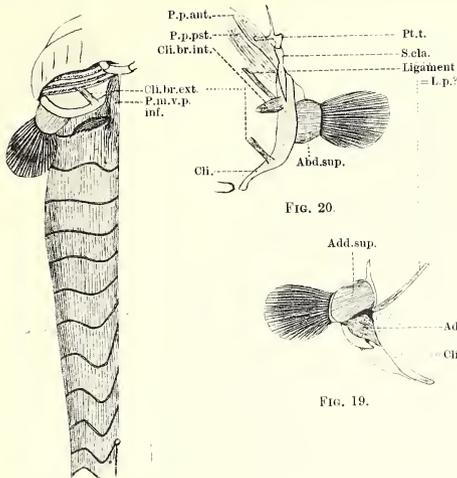


FIG. 17.

FIG. 20.

FIG. 19.

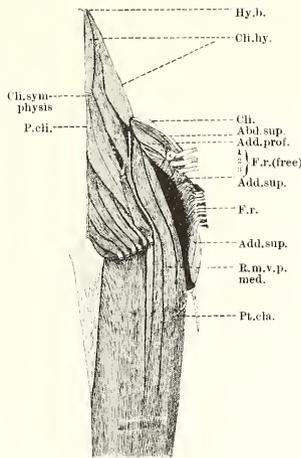


FIG. 21.

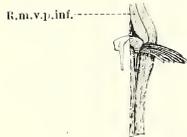


FIG. 18.

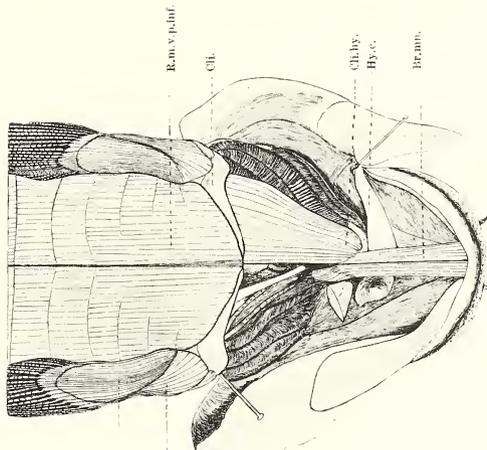


FIG. 23.

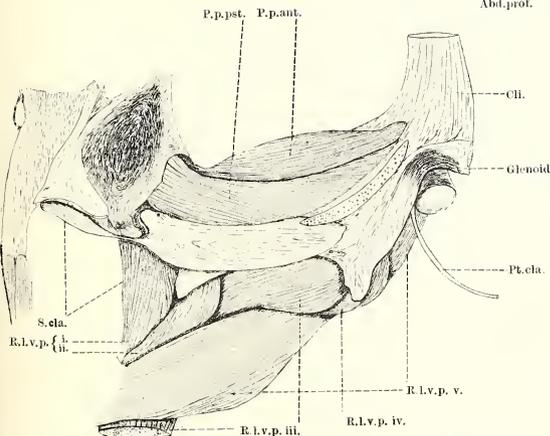


FIG. 22.

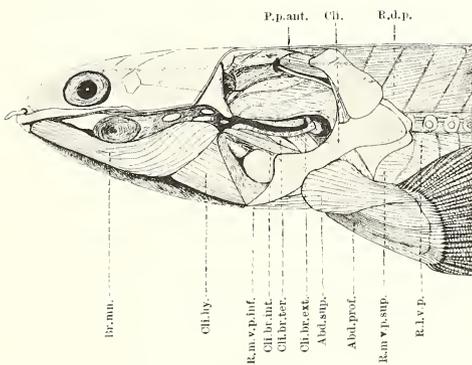


FIG. 24.



XXII.—The Morphology of the Stele of *Platyzoma microphyllum*, R. Br. By  
 John McLean Thompson, M.A., D.Sc., F.L.S., Lecturer on Plant Morphology,  
 Glasgow University. (With Three Plates and Three Figures in the Text.)

(MS. received February 3, 1919. Read February 3, 1919. Issued separately September 29, 1919.)

That the stelar problem considered in this paper may be more clearly visualised, it will be well to divest of purely theoretical considerations the facts of stelar structure already known for *Platyzoma*, and to summarise such structural features as bear on the subject in hand.

In the first account of *Platyzoma* given by ROBERT BROWN in 1810 (1), the habit of the stem and heterophyllic leaves, and the general form and position of the sporangia, were alone described. But in 1832 (2) a rough analysis of the structure of the stem was added, and the tubular nature of its stele was recognised. No material contribution to the knowledge of the stelar structure was made until 1893 (3), when Dr POIRAULT described the histology of the stele as shown by a small fragment of stem. In this material there was a sclerotic pith completely surrounded by an endodermis, outside which lay a zone of parenchyma surrounded by a broad ring of parenchymatous xylem. At the periphery of the xylem there was a narrow zone of phloëm surrounded by a large-celled pericycle and an outer endodermis. Neither leaf-gaps nor perforations were found in the stele, and accordingly the complete isolation of the pith from the cortex was recognised.

Fuller information regarding the stele was provided in 1901 by Mr BOODLE (4). In particular, he described the origin of a leaf-trace by the nipping off of a group of phloëm- and xylem-elements from the stele. The leaf-trace thus initiated departed from the stele without the formation of a leaf-gap affecting the endodermis, and it was noted that frequently the exit of a leaf-trace scarcely affected the stelar-xylem beyond forming in it a small external pit. "The nearest approach to a true leaf-gap" which was observed was a parenchymatous ray running almost radially athwart the xylem-ring, but "longitudinal sections through the insertion of a leaf-trace did not show any passage of leaf-trace-parenchyma towards the centre of the stele."

In 1916 (5) I described at some length the stelar structure as shown in part of a single specimen of *Platyzoma microphyllum*. From the central stele there departed a close succession of leaf- and root-traces. The leaf-traces varied considerably in size. The largest originated mainly from the upper surface of the stele, the smaller sprang from the sides and lower surface. The majority of the root-traces were attached to the lower surface of the stele. The pith was bulky and sclerenchymatous, and—as in the preparations of POIRAULT and BOODLE—was surrounded by

an uninterrupted endodermis which was immediately followed by a few layers of large-celled parenchyma. This parenchymatous zone was followed on its outer surface by a ring of xylem which varied in thickness as one passed from the upper to the lower surface of the stele. On its upper side the xylem-ring was thin; on its lower side it was relatively thick. The xylem was composed of scalariform tracheides together with chains and groups of parenchymatous cells which followed irregular courses between the tracheides, and which fused and branched repeatedly. The xylem was roughly divisible into two concentric cylinders according to the dimensions of the tracheides and the distribution of the parenchyma. The inner cylinder was composed of wide tracheides associated with numerous chains and masses of parenchyma, and formed the essentially parenchymatous part of the xylem. The outer cylinder was composed mainly of small tracheides which were closely packed together. Parenchyma did not bulk largely in the organisation of this outer cylinder, the chains and groups being usually short and narrow, and their component elements were few. This outer cylinder supplied the xylem to the traces of the leaves and roots. The difference in xylem-thickness between the lower and upper sides of the stele was due mainly to a massing of parenchymatous inner xylem towards the lower surface of the stele. The inner xylem fluctuated from point to point either in the direction of increase or of decrease. The greatest increases were in those regions where the departing traces were most crowded; on the other hand, the inner xylem was usually less prominent in those portions of the stele where the traces were large and scattered.

The phloëm followed almost immediately upon the outer surface of the xylem, and was separated from the xylem locally only by a single layer of small parenchymatous cells. It varied in bulk from point to point, but seldom exceeded five layers in breadth. It was composed entirely of typical fern sieve-tubes, and was interrupted only at those points where leaf- and root-traces were departing. The phloëm was followed externally by a large-celled pericycle of three to four parenchymatous layers, and beyond this was a continuous outer endodermis. These features are in complete harmony with those described by POIRAULT and BOODLE.

In the formation and departure of both large and small leaf-traces one general method was adopted. The first indication of the formation of a leaf-trace was the marking-out of a peripheral tangential band of tracheides from the outer xylem-cylinder. Beneath this tracheidal band a definite mound of parenchyma appeared, while outside it the phloëm, pericycle and outer endodermis were gently curved. As the band of xylem became more distinct and arched, the phloëm upon its convex face became thinner. The xylem-band then freed itself from the stelar-xylem, and passed out as the arched xylem of a leaf-trace. In some cases it severed its connections with the stelar-xylem simultaneously on both sides; in others it freed itself more rapidly on one side than on the other. In either case, while the phloëm

clothing the leaf-trace-xylem on its outer surface had become thinner, no diminution of phloëm took place at the points where the leaf-trace-xylem had freed itself. In point of fact, no sooner had an edge of the leaf-trace-xylem become free than phloëm began to appear in the gap which separated it from the stelar-xylem, and as the gap widened a sheet of phloëm appeared in the parenchymatous mass beneath the leaf-trace-xylem. This sheet of phloëm was an inward continuation of the stelar-phloëm beneath the departing leaf-trace-xylem. It was destined to meet a similar phloëm-sheet projecting through the gap which separated the leaf-trace-xylem from the stelar-xylem at the other edge, and when these phloëm-sheets had met and fused, a continuous sheet of phloëm was spread once more over this portion of the stelar-xylem. Meanwhile the local depletion of the outer xylem had been corrected, and the "external pit" had been obliterated.

While these structural changes were proceeding, the leaf-trace-xylem and its accompanying crescent of phloëm had continued their outward course, and the leaf-trace-phloëm had become free from the stelar-phloëm. The pericycle and outer endodermis had been moved outwards to accommodate the xylem and phloëm of the leaf-trace, and when the limit of this accommodation was reached, the leaf-trace possessed a crescent of xylem with phloëm on its convex surface and around its margins.

When the gap in the peripheral cylinder of stelar-xylem had been repaired, and phloëm again covered the xylem, a new endodermal formation appeared on both sides of the departing leaf-trace. Endodermal cells spread obliquely inwards from two points upon the arched outer endodermis, and having spread inwards, they united to establish a continuous endodermal wall which completely excluded the leaf-trace from the stele. No sooner had this endodermal formation been completed, than the outward arched portion of the outer endodermis which had accompanied the other components of the leaf-trace on their outward course became free as a crescentic band following the general outline of the trace. As a consequence of these modifications the endodermis of the free leaf-trace was at this stage incomplete, being maintained upon the outer side of the trace, but absent from the inner side. This condition was not long maintained. An inner band of endodermal cells soon appeared completing the leaf-trace-endodermis upon its inner side. *It was then evident that in the process of leaf-trace-formation and -departure, the inner endodermis was in no way involved; and further, there existed no point where the stele was not entirely enclosed by an outer endodermis. Not only has it been demonstrated that in this plant—so far as the materials examined are concerned—there existed no ground-tissue-connection between the cortex and pith, but also that no connection existed between the cortex and the pericycle at the point of final liberation of the leaf-trace into the cortex, or at any other point. The possibility of such a connection had, in fact, been removed by the formation of the fused endodermal sheets as described above.*

It frequently occurred that when the liberation of a leaf-trace made a heavy drain on the tracheides of the outer cylinder, so that the parenchymatous inner xylem was locally in direct parenchymatous connection with the parenchyma beneath the leaf-trace-xylem, a parenchymatous bridge appeared in transverse section passing athwart the xylem-ring. But many chains of parenchyma traversed the inner xylem from side to side at points other than the insertions of leaf-traces, and in not a few instances were continued almost to the periphery of the outer xylem-cylinder. Where the latter was locally parenchymatous or thin these rays were sometimes seen in transverse section to be continuous from the inner to the outer surface of the xylem. The rays were usually narrow and followed varying courses, and, in branching, ran in obliquely longitudinal directions, both backwards and forwards in the stem. *In no case observed did they disturb, or threaten, the unbroken continuity of the inner and outer endodermal bands.*

From the above account it will be apparent that no leaf-gaps were found in the length of stem examined, and that the local depletion of the outer xylem-cylinder, or a parenchymatous development within it, led to the formation of rays which traversed the xylem from side to side, and that since such local depletions of the outer xylem-cylinder were unavoidable at the points of departure of leaf-traces, it was at these points that continuous rays were most frequently seen in transverse sections of the stele.

No special interest was presented by the origins of the root-traces. The latter were restricted to the lower surface and lower portions of the sides of the stele. They originated like the leaf-traces by a protrusion of the outer xylem-cylinder, and frequently coincided with xylem-rays, but in departing they created no gaps in the stelar ring by which direct continuity of pith and cortex could be established.

The facts thus summarised have been fully illustrated in Plates I, III, and IV of the memoir mentioned above (5). With the facts recorded by Dr POIRAULT and Mr BOODLE, they provide the only record of stelar structure which has been made public for *Platyzoma*. They bear only one interpretation, namely, that *in the materials so far investigated the stele comprises a conductive cylinder with both outer and inner endoderms. It is devoid of leaf-gaps and perforations, and includes centrally a pith completely isolated from the cortex. The phloëm is present only on the outer face of the xylem.* The stelar structure is of the so-called ectophloic-siphonostelic type.

This curious stele has been the subject of some discussion, and it will be well to draw together and briefly consider the theoretical statements which have been made regarding it. In the memoir already referred to (3), Dr POIRAULT considered that the stelar structure of *Platyzoma* might perhaps be brought in line with that of a *Engleichenia*. In explanation of this view he suggested that *the pith is the result of confluence and final isolation of a series of foliar sclerotic pockets.* This conception arose from the fact that in the leaf-trace of certain *Gleichenias* a mass of

decurrent selerenchyma is gradually surrounded by the leaf-trace as the latter is followed downwards, so that a deep sclerotic pocket is enclosed by the tubular portion of the trace and appears, in transverse section, completely isolated from the cortex. "If now," he continues, "we *imagine* that, the length of the internodes diminishing, the leaves of a *Eugleichenia* approach each other closely, the base of each one of these being the seat of formation of a pocket, one can *conceive* the coalescence of these closely meeting formations leading to a general inclusion which will be enclosed in the stem like that seen in *Gleichenia polypoides*, and the resulting structure will be *very near* to that seen in the stem of *Platyzoma*." \*

It will be apparent that Dr POIRAULT *imagined certain non-existing conditions as fulfilled in a Eugleichenia*, and that he merely contemplated a possible explanation for *Platyzoma*, for which no adequate supporting evidence was provided.

This idea of the origin of the pith of *Platyzoma* was taken up in 1897 by Dr JEFFREY (6). On page 869 of the report of the British Association meeting it is stated:—"Among the *Gleicheniaceæ* we have in *Martensia* the cortex sending parenchymatous strands into the vascular axis of the stem down through the channelled leaf-traces. In *Gleichenia* and *Platyzoma* these are *completely cut off* from the outside cortex, and we have a completely included pith similar to that present in *Osmunda*. *The pith in these forms is in reality extrastelar*, but no longer communicates with the peripheral cortex." Thus a possible explanation advanced by Dr POIRAULT for the stele of *Platyzoma* was transformed by Dr JEFFREY into the true and actual explanation, even although no structural evidence was advanced which would justify dogmatism. For it will be noted that a direct ground-tissue-connection between the cortex and stelar pith of *Platyzoma* has not been recorded by any investigator, and accordingly the cutting of such a connection has not been demonstrated even in the phyletic sense.

In 1900 (7) the extremity of this position was modified, though indeed no further facts had emerged regarding this plant. Thus on page 7 of this paper it was stated: "It has further been rendered *probable* by the interesting investigations of POIRAULT that the apparently medullated monostelic central cylinder of the stem of the *Gleicheniaceous* genus *Platyzoma* also possesses a pith derived from the extrastelar fundamental tissue."

In 1901 (4) Mr BOODLE, after personal observation of the stelar structure, wrote as follows:—" *Platyzoma* appears to be a xerophytically reduced form in which the leaf-traces have become small and crowded; it is *perhaps probable* that it may have been derived from a solenostelic form, by obliteration of the leaf-gaps and disappearance of the internal phloëm of the stele. This view is, I believe, held by Dr E. C. JEFFREY. It is possible, on the other hand, that *Platyzoma* may have been derived from a protostelic *Gleichenia*, and its structure might then be due to the formation of a pith and internal endodermis." An extrastelar origin for the pith of *Platyzoma*

\* The italics throughout this paper are those of the writer of this memoir.

was thus contemplated by Mr BOODLE as *perhaps probable*, but an intrastelar origin within an original protostele seemed also *possible*.

In thus stating the views which seemed alternative, Mr BOODLE clearly showed that the structural facts—to which he was the chief contributor—were inadequate foundations for a confident opinion as to the true origin and nature of the medullated stele of *Platyzoma*.

Mr BOODLE'S work on the anatomy of the *Gleicheniaceæ* was followed in 1902 by a paper by Dr JEFFREY on "The Structure and Development of the Stem in the *Pteridophyta* and *Gymnosperms*" (8). It included no new observations on *Platyzoma*, but the stele was said to closely resemble that of *Osmunda cinnamomea*, since it is a collateral stelar tube with an internal endodermis. The author further remarked: "Through the kindness of Dr D. H. SCOTT he\* has had the opportunity of examining some sections of a dried stem of this species.† *The foliar gaps are nearly degenerate* in this small extremely xerophytic fern. It would be interesting to investigate branching specimens of this species if such occur, to discover whether the internal endodermis is continuous with the outer one through the ramular gaps. It seems not improbable that this may turn out to be the case." At a later point in the present paper it is shown that although the stem of *Platyzoma* is frequently branched, *no ramular gaps exist* in the materials examined; the pith has always been found to be completely isolated from the cortex, and *no connection has been seen between the outer and inner endodermal sheaths*. The suggestion contained in the concluding remarks of the above quotation may therefore be set aside as disproved. But the statement that "*the foliar gaps are nearly degenerate*" remains to be considered. It clearly implies that some observation has been made from the sections referred to suggesting the presence of reduced or degenerate foliar gaps, and, if justified, might aid materially in the interpretation of the stele. For it will be evident that the presence of nearly degenerate foliar gaps would be strong evidence in support of a belief that the so-called ectophloic siphonostele of *Platyzoma* is the result of reduction, and was at least preceded at some point in the ancestry by a siphonostele in which foliar gaps were well defined, so that the pith and cortex were in direct connection through them. Dr SCOTT and Mr BOODLE have kindly put at my disposal the sections already examined by Dr JEFFREY. Each one possesses parenchymatous xylem-rays like those already described in the preface of this paper. At several points leaf-traces are departing from the stele, and in some instances a parenchymatous ray links the parenchyma beneath the leaf-trace-xylem with the parenchymatous zone immediately inside the xylem-cylinder.

It was from such sections as these that Mr BOODLE'S analysis of the vascular construction was made, and it was probably from one of them that his illustrations of a departing leaf-trace were taken (figs. 33, 34, pl. xxxix), "to show the

\* Dr JEFFREY.

† i.e. *Platyzoma*.

nearest approach to a true leaf-gap met with." In them no leaf-gap affecting the endodermis is present, and the only structures which might possibly be interpreted as nearly degenerate leaf-gaps are the parenchymatous xylem-rays immediately internal to the leaf-trace-xylem. The most obvious ray of this kind which I have found in these sections is represented in fig. 26 of the present paper. By themselves such rays can scarcely be held to prove the prior existence of foliar gaps of which they are the degenerate relics, and accordingly they cannot reasonably be brought into court as proof of the present reduced state of the stele of *Platyzoma*. If such xylem-rays are to be considered the almost degenerate relics of leaf-gaps, all prominent rays which completely or almost completely traverse the xylem-ring might similarly be considered the degenerate relics of stelar gaps of one kind or another. However true it may prove to be that "there is ground for the belief that the solenostele may give rise by reduction to a modification not distinguishable in any way from the medullated monostele of VAN TIEGHEM" (8), the stelar reduction indicated above has not been proved for *Platyzoma*. And further, there will be a natural hesitation in accepting as justifiable Dr JEFFREY'S comprehensive statement that "the simplest view, and that most in harmony with all the facts, seems to be that the medullated monostelic central cylinder has been derived from an ancestral siphonostelic condition with internal phloëm by reduction" (8). For the stele of *Platyzoma* is a medullated monostelic cylinder which has not been shown to have possessed at any time internal phloëm and foliar gaps.

The reduction theory was supported by Mr TANSLEY in 1908 (9), and it may be well to quote at length his remarks. On page 44 of his Lectures he wrote: "*Platyzoma* has a curious and rare type of stele containing a pith surrounded by an endodermis but no internal phloëm, and with quite small collateral leaf-traces whose departure does not break the continuity of the vascular ring as it does in the normal solenostelic type." And on page 106, while discussing the interpretation of the Osmundaceous stele, he stated that "ferns which have a continuous internal endodermis and no internal phloëm are decidedly rare. We have such a case, however, in the Gleicheniaceae genus *Platyzoma*, and the stele of this plant also resembles that of the *Osmundaceæ* in having no leaf-gaps putting the cortex in connection with the pith, the leaf-traces departing from the outer surface of the xylem-cylinder somewhat as in the simpler Osmundaceous types. *There is good reason for considering Platyzoma as an instance of reduction.*" On page 108 it was stated: "It is no doubt conceivable that *Osmunda skidegatenensis* is reduced from a normal dictyostelic type in which the leaf-traces have secondarily come to depart from the outer face of the xylem-cylinder, their internal phloëm has ceased to be connected with the internal phloëm of the stem, and the leaf-gaps have become very narrow. Some such process of reduction as this has very likely occurred in *Platyzoma*." And lastly, on page 134 he wrote: "If the reduction of leaf-traces relatively to the stele is great enough, a siphonostelic form like *Platyzoma* may have no leaf-gaps."

I have quoted these remarks in full so that the reader may see more clearly that they are not the bearers of new morphological facts, but are merely the restatement of the reduction theory already advocated. But they entail an implication which may be briefly considered, namely, that *in an organism under xerophytic conditions simplification or reduction of the axile stele may be expected to take place, and in the case of *Platyzoma* has actually occurred in the manner indicated above.* Such a suggestion may gather strength from the facts that the leaves of *Platyzoma* are densely crowded upon the axis, and many of the leaves are of reduced and remarkably modified type (5). The axis is then probably of a condensed and slow-growing type, as might be expected under xerophytic conditions. But from this it does not seem to follow reasonably that telescoping of the stele has taken place in the phyletic sense with the obliteration of foliar gaps. And further, even though it were proved that stelar modifications had arisen in *Platyzoma* under xerophytic conditions, no structural evidence has been advanced to show that the stele of *Platyzoma* was at any time solenostelic. Much less has it been shown that in any solenostelic fern under xerophytic conditions stelar reduction has taken place and has followed the lines indicated, namely, that leaf-gaps have been obliterated and inner phloëm lost.

But there is another aspect of this question which must be considered, for it lies behind Mr BOODLE'S alternative view that "*Platyzoma* may have been derived from a protostelic *Gleichenia*, and its structure might then be due to the formation of a pith and internal endodermis." This suggestion may justifiably be transformed so as to be read that *the present medullated monostelic condition of *Platyzoma* is the direct result of medullation of an original protostele which has not acquired leaf-gaps during transformation.* It is to be granted at once that this alternative upgrade view stands, as does the reduction theory, not only "not proven," but also so far unsupported by facts of observation. It presumes that the pith and internal endodermis were created *de novo*, whereas the reduction theory presumes intrusion of the cortex and outer endodermis into the stele through leaf-gaps, the formation of a pith of purely cortical origin, and other modifications which culminated in the establishment of a typical solenostele; and when this had been accomplished—according to the reduction theory—the leaf-gaps were obliterated and the inner phloëm completely disappeared. The implication of Mr BOODLE'S view of the stele of *Platyzoma* is that *the present medullated monostelic state is the high-water mark of elaboration from an original protostele reached either under xerophytic conditions or independently of them.* If this view could be reasonably supported by structural facts, it would merit the same consideration as would be due to the reduction theory if structural evidence of degenerate internal phloëm and of actual leaf-gaps were forthcoming.

The matter stood thus in suspense when in 1908 Dr JEFFREY'S paper entitled "Are there Foliar gaps in the *Lycopside*?" appeared (10). From it I am extracting

certain statements which seem to have a bearing on the subject in hand. On page 241 it is stated: "There are two phylogenetic types of tubular central cylinder, namely, that in which only ramular gaps are present, and that in which both ramular and foliar gaps occur." "The use of these *constant* and *characteristic* anatomical features results in the division of the *Vasculares* into two great primitive stocks—the *Lycopsida* which are cladosophonic and palingenetically microphyllous, and the *Pteropsida* which are phyllosiphonic and palingenetically megaphyllous." "The *Lycopsida* include the *Lycopodiales* and *Equisetales*; the *Pteropsida* include the *Filicales*, *Gymnosperms*, and *Angiosperms*." On page 242, in amplification of the above statement, he continued: "*Pteropsida*. Palingenetically megaphyllous vascular plants with dorsi-sporangiate sporophylls, *the tubular central cylinder when present characterised by foliar gaps or interruptions in the fibro-vascular tissue immediately above the outgoing foliar traces*." In this way it is implied that a fern possessing a tubular central cylinder like that of *Platyzoma*, devoid of foliar gaps or other interruptions in the vascular tube, is uncharacteristic for ferns, and can reasonably be regarded only as of downgrade and reduced type. The alternative upgrade view was not even considered.

This attitude was still more clearly shown in 1910 when Dr JEFFREY'S paper on "*The Pteropsida*" appeared (11). In it the "morphological status" of pith was regarded as "external tissue included by the stele in the course of evolution." On page 408 it is stated: "It appears evident, since the stelar system of the stem in the case of certain of the lower *Pteropsida* is able to include tissues and substances which are beyond question extrastelar in their origin, that no difficulty arises in regarding the pith present within the siphonostelic central cylinder of the lower as well as the higher *Pteropsida* as morphologically equivalent with the fundamental tissues of the cortex, with which it is often continuous through the gaps in the stelar walls resulting from the exit of the vascular supply of leaves and branches." "A further argument in favour of this view is the frequent textural similarity between pith and cortex, even where the former as the result of upward evolutionary tendencies is no longer continuous with the fundamental tissues without the stele." On page 412 he concludes: "It now in fact appears much more clearly than formerly that the primitive condition of the vascular system in both stem and leaf in the *Vasculares* as a whole was what the present writer has designated protostelic, *i.e.* a condition in which the fibro-vascular tissue harboured no pith. Following this condition was one in which the fibro-vascular system became transformed especially in the more progressive stem into a stelar tube lined both externally and internally with phloëm and endodermis. In the process of time the internal phloëm became degenerate, probably on account both of the absence of direct relation to the leaves and of the appearance of secondary growth, advantageously localised ultimately on the outer surface of the stele. The internal endodermis more slowly followed the internal phloëm into oblivion, and is often

found at the present time in the young individual when it is absent in the adult. (*Ophioglossaceæ*, *Equisetaceæ*, *Ranunculaceæ*.) *The pith must in all cases be regarded as a derivative of the cortex, which has become more or less completely segregated within the stele.*" These remarks contain no actual reference to *Platyzoma*, but according to their conclusion the pith of *Platyzoma* must be regarded by Dr JEFFREY as of extrastelar origin, and the stele itself as reduced so as to have lost internal phloëm and leaf-gaps, but still to have retained its inner endodermis.

I have dwelt on the published statements of those who have supported the reduction theory for the stele of *Platyzoma* so that the arguments involved might be fully understood. By reiteration rather than the support of cogent facts they have been strengthened, but they have not solved the stelar problem. I am driven to the conclusion that the reduction theory as so far stated stands merely upon unwarranted and comprehensive assumptions, and that there is no justification in the recorded facts of fern-anatomy for regarding the reduction hypothesis for *Platyzoma* as anything more than an *undemonstrated possibility*. Having regard to the recorded facts, I am constrained to maintain this position with regard to the stelar morphology of *Platyzoma* in direct opposition to Dr JEFFREY's recent statement that, "so far as the plentiful evidence in the case of the *Filicales* is concerned, it seems beyond reasonable doubt that the median parenchyma of the tubular or siphonostelic central cylinder has come from the outside, and is not the result of internal differentiation within the stele" (12).

But the object of this paper is not mere criticism of the theoretical statements which have grown around a limited body of fact. It is rather the recognition of the problems of stelar structure which await solution for *Platyzoma*, and the contribution and employment of certain new facts which have emerged from recent investigation. It was evident from the outset that the facts obtained from a few sections of the stem and from the general habit of this plant were totally inadequate to allow of a confident opinion as to the true nature and origin of the tubular stelar structure. Ample material embracing "sporeling" stages and mature plants could alone provide the fuller ontogenetic facts which are necessary. The "sporeling" stages have not yet been obtained, but through the kindness of Dr BAILEY of Brisbane Botanic Gardens a number of plants of various ages have been available for study. In most cases the stem was robust, and, though basally incomplete, measured from three to five inches in length. In all of them the apparent zonation of leaves already described was seen, and all were heterophyllic (5), (13). The majority of the larger stems were dichotomously branched, and in one instance the branching had occurred at least twice. The materials included one small and apparently relatively young plant. Its stem was more slender than that of any of the larger specimens. Basally it was incomplete, but otherwise it was a perfect specimen. It showed well the leaf-zonation, there being three groups of pinnate

leaves alternating with zones in which filiform leaves predominated. The stem of this small plant and those of a number of the larger specimens have been sectioned throughout their entire length, so that no opportunity might be lost of discovering in them a solenostelic condition, foliar gaps, or evidence of the loss of gaps and internal phloëm. The discovery of any one of these would materially affect any interpretation of the stelar state. Degenerate gaps and phloëm would undoubtedly raise the reduction theory to the plane of probability, but an actual solenostely without evidence of degeneration or reduction would be open to interpretation as the result of stelar amplification, *provided an upward progression from protostely to this kind of tubular stele could be indicated in the ontogeny*. But in any case, neither the presence of degenerate leaf-gaps and phloëm, nor the existence of the so-called ectophloïc-siphonostelic state, would provide any grounds for a belief in the cortical origin of the pith of *Platyzoma*. At most they would have demonstrated merely a connection between pith and cortex which would seem to have been broken frequently in the phyletic sense in this plant.

On the other hand, the discovery of a protostelic state giving place in the ontogeny to a well-defined medullated protostele with isolated internal endodermis and entire absence of foliar gaps and internal phloëm would lend support to the theory of upgrade development, *unless it be further assumed, without evidence from fern-anatomy, that such a protostele merely demonstrates the extent to which reduction may go*. Such a view of widespread reduction would necessitate that the internal endodermis had followed the inner phloëm and the leaf-gaps "into oblivion," with the result that a stelar structure in no way distinguishable from an original protostele was established. The supporter of such a reduction theory would be compelled to view with suspicion most fern-protosteles, for each would be open to interpretation as the result of drastic reduction from a solenostelic state or from some other type of tubular stele. The "sporeling"-structure of modern ferns—in which protostely so commonly figures—would likewise be placed under suspicion as a possible reduction phenomenon. The logical conclusions to such an attitude would be, first, to suspect everything with a pure protostele or a medullated protostele of being reduced; second, to negative ontogeny unless it shows *throughout* a solenostele or some upgrade modification thereof;\* and third, to consider solenostely and not protostely as primitive in the sense recently advocated by Dr JEFFREY, "that the tubular condition is both typical and primitive for the ferns in general, with the sole exception of those forms in which the organisation of the stele *maintains* the original protostelic state" (14). This would imply that protostely must persist throughout the entire ontogeny if it is to be considered an original protostely, and that once solenostely appeared, the original protostely was lost, and that where protostely and solenostely exist in the same individual, the latter is the

\* In discussing the stele of *Angiopteris evecta* in 1902 (8), Dr JEFFREY stated that he had examined some young plants, but "unfortunately these proved rather too young for the present purpose, since the central cylinder had as yet hardly passed into the tubular condition."

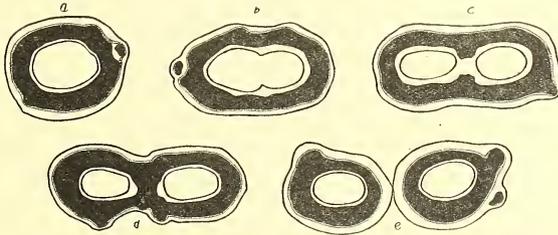
result of reduction from the former. Behind the reduction theory lies the idea that all normal ferns with tubular steles *must* have stelar gaps, for unless this be so, a fern such as *Platyzoma* with an isolated pith, if considered normal and unreduced, would be a stumbling-block to the generalisation that "the pith must in all cases be regarded as a derivative of the cortex which has become more or less completely sequestered within the stele" (11). Such a view as that advocated by the theory of the cortical origin of pith would seek to exclude the alternative view that ferns with pithed tubular steles may in certain cases illustrate a condition in which stelar gaps have not yet been formed either in the ontogenetic or phyletic sense. *But if in any fern a pith has arisen without the creation of stelar gaps, it cannot have been formed by cortical intrusion.* It may be noted further that on the upgrade theory the presence of ill-defined or scattered phloëm, or of incipient leaf-gaps, might conceivably be considered evidences of further amplification of an original protostele, provided it be granted that tissues of one kind or another can be formed where required and are not necessarily referable in origin to one original and continuous tract which has been extended and disintegrated in the phylogeny.

The stelar structure in the large specimens of *Platyzoma* will be referred to first. In each case there was throughout a well-defined pith enclosed by a continuous tubular endodermis which was at no point in connection with the outer endodermis. Neither inner phloëm nor any structure suggestive of inner phloëm was found. There were neither leaf-gaps nor evidences of the prior existence of leaf-gaps. The only points which these plants added to the facts already acquired were the following. The pith fluctuated in bulk from point to point. In some plants it was a relatively thick strand where the traces of large leaves were most numerous, and more slender where the stem bore mainly small leaves. In other plants no such fluctuations were observed, even although the leaf-zonations were well shown. In some instances the pith was sclerotic throughout; in others it was in part sclerotic, in part parenchymatous. A number of dichotomies were cut in serial sections, and in each instance the division of the stele into two followed the plan illustrated in text-figure 1. The stele of the parent stem became expanded laterally (*a*, *b*), and as preparation for division of the xylem proceeded the inner endodermis became separated into two distinct and complete tubes (*c*). Between these a bridge of xylem was established (*d*), so that the two parenchymatous cores now separated from each other were not placed in open parenchymatous connection with the pericycle. The stele then divided into two similar steles (*e*) by division of the xylem-bridge, the completion of phloëm and pericycle around the now isolated tubes of xylem, and the separation of the outer endodermis into two complete cylinders.

It will be seen that neither ramular gaps nor other breaks in the continuity of the stele existed in the materials examined, and that the pith of the parent stem, in dividing to form the pith of the branches, was not brought into contact with the cortex. The investigation of these stems has added nothing to our knowledge which

materially alters or helps to solve the problem of the origin of the pith and the nature of the stele of *Platyzoma*. On the other hand, the small specimen referred to above revealed some interesting features. These will now be described in advancing order as they presented themselves in the series of sections into which the stem was cut from its incomplete base to the apex. The series of illustrations of this plant given in the accompanying plates have been prepared by camera-lucida drawings, and are made to a uniform magnification.

At the broken base of the stem the stelar structure was as in fig. 1. The outer endodermis (O.E.) was continuous, and root- and leaf-traces were being liberated (R.T. and L.T.). There was a narrow band of phloëm (Ph.) around the bulky xylem. The latter was divisible into a narrow peripheral zone of small elements, and a mass of inner parenchymatous xylem much more bulky towards



TEXT-FIG. 1.—Diagrams of the structure of the stele of *Platyzoma* at successive points in a bifurcating stem, as seen in transverse sections. Both outer and inner endodermis are represented by black lines; phloëm is hatched and xylem is solid black. Pericycle, inner parenchyma, and pith are white. ( $\times 12$ )

the lower than the upper side of the stele. The xylem enclosed a mass of parenchyma, the central part of which was surrounded by a small continuous endodermis (I.E.). This condition was followed by that shown in fig. 2. The bulky xylem was maintained, and apparently isolated tracheides were found in the mass of parenchyma which it surrounded. The inner endodermis had closed down to form a narrow tube enclosing only a few rows of parenchymatous cells. A little in advance of the point where this latter condition was seen the stelar structure was as in fig. 3. The inner endodermis had been reduced to a vanishing-point, so that it appeared in section as a small group of endodermal cells enclosing no parenchyma (I.E.). In the immediately succeeding sections the stele appeared as in fig. 4. The inner endodermis had ceased to exist at this point, and a stelar structure in no way distinguishable from that of a medullated protostele had been established. This condition was followed almost immediately by that shown in fig. 5. The pith was no longer bulky, and a stelar structure not far removed from an almost solid protostele was seen. As the series was followed forward, the condition illustrated in fig. 6 was reached; an irregular but continuous medulla had been created by a

continuation of parenchymatous tissue from the immediate neighbourhood of the slender persistent medulla into the mass of parenchymatous xylem. Within this expanded pith there then appeared an irregular and incomplete endodermal tube and an isolated chain of endodermal cells (I.E.). The resulting structure is illustrated in fig. 7. This condition led on to that shown in fig. 8; the inner endodermal tube had become closed so as to isolate a body of parenchyma from the main medullary mass. The independent chain of endodermal cells was still present in the sections. Further forward the inner endodermal tube became open once more, and new endodermal formations arose within the medulla. The resulting structure appeared in section as in fig. 9. By the opening of the inner endodermal tube the parenchyma which it surrounded at the point immediately preceding was again placed in open communication with the main medullary mass. An independent row of endodermal cells lay within the partially enclosed parenchyma, and a sheet and slender tube of endodermal nature had arisen towards the opposite side of the pith. A number of fluctuations in the disposition of the inner endodermal formations followed, but these soon gave place to the arrangement shown in fig. 10. A wide cylinder of inner endodermis was now clearly defined, but locally it was imperfectly differentiated, while isolated endodermal cells appeared sporadically in various situations. One such cell is shown within the parenchyma enclosed by the inner endodermal tube. As the series was followed still further forward the sporadic endodermal formation ceased. The wide and continuous inner endodermal tube was maintained for some distance, though still locally imperfectly differentiated (fig. 11). But a return to an ill-defined condition was soon made, the continuous cylindrical inner endodermis giving place to an interrupted tube within which detached chains of endodermal cells were enclosed. The resulting structure appeared in section as in fig. 12. The inner endodermal formation had been fundamentally disrupted. These transformations prefigured the condition shown in fig. 13. The inner endodermal formation had been resolved as the sections were followed forward into a narrow and almost complete tube enclosing a large body of the medulla, and into an independent irregular group of cells. This latter group was found to diminish and finally to end abruptly in the sections immediately succeeding the one figured (fig. 13). The condition depicted in fig. 14 was subsequently established, the persisting inner endodermal tube having been completely formed though narrowed considerably. Around the inner endodermis a general development of parenchymatous inner xylem had been organised. It will be apparent that at this point the medulla was again diminishing, and the inner endodermis was in fact once more in process of being eliminated. The chief steps in this elimination as shown in the sections are represented in figs. 15, 16. The inner endodermis became a slender tube within a very restricted mass of pith (fig. 15), and when the vanishing point for the endodermis was passed, a stellar structure in no way distinguishable from a medullated protosteles was again established (fig. 16). The purely parenchymatous

pith thus formed expanded rapidly as the advancing series was followed, and within it a new endodermal formation arose (I.E., fig. 17). It passed quickly from this irregular and ill-defined condition to that seen in fig. 18. At all points the inner endodermal cylinder had become complete and fully differentiated. It embraced a large body of the medulla, part of which had become sclerotic. Further forward the stele as a whole underwent diminution (fig. 19), but later it expanded to the condition shown in fig. 20, having a wide and complete inner endodermal tube enclosing a somewhat sclerotic portion of the pith. At this point the stele showed the general structure which has hitherto been known for *Platyzoma*.

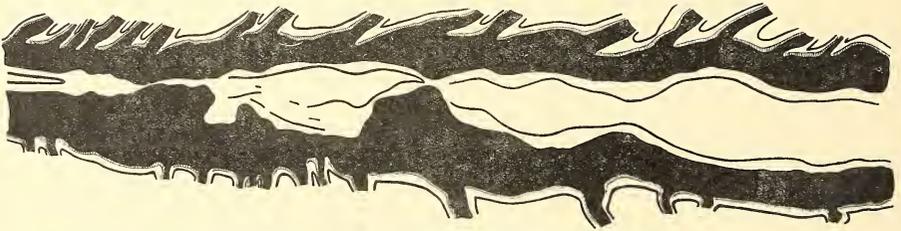
It will be seen that so far as the description of this stem has gone, the inner endodermis has twice been narrowed down to a vanishing point, so that a stelar structure not distinguishable from a medullated protosteles has been established locally. In the second place, it will be clear that with the increase in the medullation of the two protostelic zones thus formed an inner endodermis has arisen *de novo* within the pith itself. In both instances the diminishing endodermal tube has retained an unbroken identity to the end, but in the process of endodermal-re-creation there has been at first a marked indefiniteness. The new endodermis has not appeared within the growing pith as its predecessor vanished from the diminishing pith, for there is no single point of endodermal-re-creation from which an immediately tubular endodermis has expanded, whereas there was in both instances a single point to which the decreasing tubular endodermis was narrowed. It will be further noted that, in the first instance of re-establishment of the inner endodermis, the fluctuations preceding the establishment of a clearly tubular endodermis were prolonged and varied, but in the second instance they were few and comparatively simple. The two zones in which the protostelic state existed, and that portion of the stele where considerable constriction occurred (fig. 19), were the main points of origin of the small leaf-traces, while those zones which possessed a large pith gave rise to the majority of the large leaf-traces. It was difficult to determine the destination of each leaf-trace even in a careful reconstruction of the stem, but the opinion was formed that the protostelic zones coincided roughly with two of the groups of small leaves.

The general construction of the most interesting portion of the stele of this plant is illustrated in text-fig. 2. It purports to represent in slightly simplified form the general proportions and relationships of the component tissues as seen in median section. The outer and inner endodermal layers are indicated by black lines, both pericycle and pith are white, phloëm is hatched, and xylem is solid black. It will be seen that throughout the greater part of the stele thus represented, the protostelic zones show conspicuous increase of the xylem towards the lower surface of the stele. An examination of the figures given in the plates of this paper will show that this increase is due to marked local increase of the parenchymatous inner xylem. Throughout the entire length of stem so far described neither foliar gaps nor

indications of stelar gaps of any kind were found. The same remark applies to the apical portion of the stem which remains to be considered.

This younger portion of the stem retained to its apex the well-defined tubular stele, and accordingly only a small part of its stele is represented in text-fig. 2. With a number of other apical portions of stems it was examined throughout so as to demonstrate the steps of stelar differentiation from the apical meristem. In all essential points the differentiation which it showed was in agreement with what was seen in the other materials. The description given for it will suffice for all. The stelar structure may conveniently be read backwards from the apex to the point of complete stelar differentiation. In this way the entire stelar structure of the plant under consideration will have been described.

Close to the apex of the stem the stele appeared in section as in fig. 25. Both

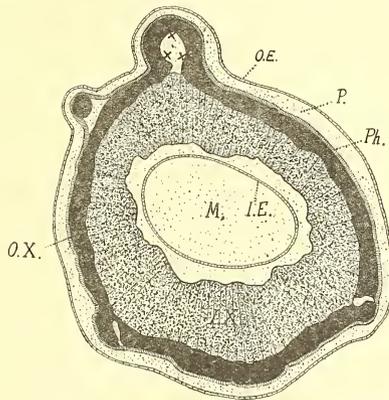


TEXT-FIG. 2.—Diagram of the structure of a portion of the stele of the small plant of *Platyzoma* described in the text and illustrated in the plates. Both outer and inner endodermis are represented by black lines; phloem is hatched and xylem is solid black. Pericycle, inner parenchyma, and pith are white. The diagram represents the general arrangement of tissues as seen in what would have been a median longitudinal section of the stele. ( $\times 16$ .)

outer and inner endodermal sheaths were clearly defined. Between them lay the still imperfectly differentiated pericycle, phloem, xylem, and inner parenchyma. Xylem-differentiation had commenced intermittently at the periphery of the xylem and in the nascent traces, but the inner xylem was not yet clearly distinguishable. No stelar protoxylems were seen. Further back the condition represented in fig. 24 was found. The outer xylem was almost completely differentiated, but though the large tracheides of the parenchymatous inner xylem were clearly indicated, their lignification had only just commenced. The differentiation of the inner xylem progressed mainly centripetally as the lignification of the outer xylem approached completion (fig. 23), and soon reached the stage represented in fig. 22. From this point it was a mere step to the fully differentiated state depicted in fig. 21. The general centripetal differentiation of the inner xylem and the ill-defined sequence in the outer cylinder were shown in all the materials examined. Although no well-defined stelar protoxylems were recognised, typical spiral protoxylems were occasionally observed in the departing leaf-traces. An example of this is represented in fig. 27. It shows an almost median and two intra-marginal protoxylem-groups which, if continued down as the leaf-trace-xylem becomes completely concurrent with

the outer stelar xylem, would occupy the positions indicated by the three crosses in text-fig. 3, and if projected into the stele itself, could not fail to have a mesarch position. The theoretical position of the stem-protoxylems would therefore be mesarch.

It will be evident that the tubular portions of the stele of *Platyzoma* are constructed on the plan indicated in text-fig. 3, with outer and inner endodermis (O.E. and I.E.), between which lie in centripetal sequence pericycle (P.), phloëm (Ph.), outer xylem (O.X.), inner xylem (I.X.), and inner parenchyma. Internal to the inner endodermis is what is generally recognised as the pith (M.), but it will be clear



TEXT-FIG. 3.—Diagram of structure of medullated stele of *Platyzoma* as seen in transverse section. O.E., outer endodermis; I.E., inner endodermis; P., pericycle; Ph., phloëm; O.X., outer xylem; I.X., inner xylem; M., medulla. ( $\times 50$ .) The three crosses indicate the positions of the leaf-trace protoxylems.

that if the pith as a whole is in this case of purely intrastelar origin, the inner parenchyma immediately within the parenchymatous inner xylem is a portion of the original pith which has not been included within the inner endodermis. On the other hand, if the pith were of cortical origin, then only the ground-tissue enclosed by the inner endodermis could reasonably be regarded as pith, and the inner parenchyma above referred to would be open to interpretation as the intrusive extension of the pericycle. There seems no ground for the latter belief in the facts now recorded. The outer and inner endodermal cylinders have been shown to be entirely independent of each other, the former being invariably maintained inviolate while the latter has fluctuated and locally vanished, and neither fully developed nor degenerate stelar gaps have been found. Throughout the entire plant which has just been considered the tissues were apparently normal in form and differentiation, and no grounds were found for considering the plant abnormal or perverted in any of its parts.

The fuller facts of stelar structure have now been recorded. It remains to consider the effect of their recognition upon the stelar problem. It is at once admitted that they are inadequate to allow of a solution of the problem, for they lack the support of the evidence of the "sporeling"-structure, and of the earlier ontogenetic stages generally. But the following points have been proved :—

- (i) *Platyzoma* is at points protostelic.
- (ii) It has been shown to greatly augment an attenuated pith *from within* the stele; on the other hand, the pith may be drastically diminished.
- (iii) It has been shown to develop entirely from within the stele an inner endodermis around a portion of the pith.
- (iv) It has neither foliar nor ramular gaps; nor does it show any structural evidence of having possessed at any time either stelar gaps or internal phloëm. Thus an original solenostele has not been demonstrated.

Among the results of this investigation there is not one fact which could reasonably be considered evidence in favour of the reduction theory of the stelar structure, *unless it be that protostely recurs in those zones which are apparently the bearers of the majority of the small leaf-traces*. This alone could be considered evidence of reduction if it be granted that the stelar structure is liable to be reduced under xerophytic conditions. It might be held to demonstrate the extent to which reduction may go. But no evidence of the original solenostely upon which the reduction theory hangs has emerged; much less have the materials shown "pocketing" in an original protostele by which the cortical ground-tissue has "invaded" the protostele and established a pith. It will be evident that if the course of stelar transformation and reduction proposed for *Platyzoma* has actually been followed in descent, this is the first recorded example of a fern which has reached solenostely by amplification of an original protostele, and has returned to protostely by reduction. On the other hand, it will be clear that, even supposing the so-called ectophloëisiphonostely of *Platyzoma* be the result of reduction from solenostely, no evidence has been advanced to show that this solenostely arose by a process of cortical "intrusion." If, as seems the case in the materials discussed above, both diminution and augmentation of pith and inner endodermis are purely intrastelar phenomena, there is no initial reason why inner phloëm should not arise within a medullated protostele not only where required, but also independently of the outer phloëm. But whatever be the possibilities, the fact remains that in promulgating their view of the stelar structure of *Platyzoma* the advocates of the reduction theory have seen neither the solenostelic stage they presume existed nor the protostelic stage which has been described above, and from which arises a purely intrastelar pith. It will be of interest to see what bearing the fluctuations of the inner endodermis above recorded may have on the problem raised by the isolated endodermal spindles which Mr BOODLE has recorded from the stele of *Schizæa dichotoma* (15).

But if the reduction theory has received little support from the recorded facts, on the other hand the theory of upgrade internal differentiation has not been proved, though the general trend of the stelar fluctuations which have been described in these pages might reasonably be considered in its favour. Thus the fact that within a protostele a pith has been shown to grow and to become more or less included in an inner endodermis created *de novo*, points directly to the course which a supporter of the theory of intrastelar origin of the pith in *Platyzoma* would expect to be followed in the ontogeny. *In the case described such an intrastelar development would be considered to have occurred at least three times, and on all but the last occasion had not been maintained, but had reverted directly to the original protostelic state.* The inference would be that any one of three definite states may exist in the stele of a fern, and that these states are continuous in the evolutionary sense. First, *the original protostely may persist undisturbed throughout the entire ontogeny.* Primitive protostelic ferns would be examples of this. Second, *the original protostely may be transformed at an early stage in the ontogeny once and for all into one or other of the more elaborate stelar states.* Third, *the original protostely may recur in the ontogeny in ferns in which the advanced stelar state is not yet permanently established.* Whatever be the actual course of stelar amplification followed in individual cases, the second state appears to have been widely exemplified in modern ferns. *Platyzoma* may provide an illustration of the third and apparently exceptional state in which the stelar structure of the ancestry has not yet been definitely restricted to the "sporeling" stages, but tends to persist in the mature organism. If this be so, then the structural evidence dealt with above may indicate a reminiscence of the steps taken in the initial transformation of the ancestral protostele. Such steps would be, first, the growth of the pith within the stele itself, and second, the inclusion of the bulk of the pith within an independent internal endodermis formed *de novo*. It has been shown by Dr LANG that endodermal cells may be formed where required in the stem of *Helminthostachys* (16). And further, FLASKAEMPER has shown that pith may be locally present and locally absent in one and the same root according to the general conditions provided for the organism (17). He found that after a seedling of *Vicia* had been grown until the radicle had begun to elongate, if the cotyledons were removed, the growth of the plant was checked, and the root, pithed in its older part, was devoid of pith in the part subsequently formed. But when the plant had become strong under continual exposure to favourable conditions, a pith was reorganised in the later parts of the same root. In like manner the stelar pith of the stem of *Platyzoma* may be viewed as open to fluctuation either by decrease or increase under the varying conditions of life, and need not be regarded as the relic of a cortical intrusion which has persisted under xerophytic conditions. A parallel may possibly be found in the case of *Lepidophloios Scottii*, Gordon (18), in the stem of which the pith may come and go, though indeed no evidence has been advanced to show that in it this fluctuation is a sign of reduction.

It seems more reasonable to raise ontogenetic evidence—even though incomplete—to the place of honour in the interpretations of adult structure, than to reject it in favour of distant lateral comparisons which necessitate mere assumptions. But it may be objected that the creation of an inner endodermis entirely independent of its outer correlative is a most exceptional occurrence, and that there is no apparent and reasonable need for it in a stele which is completely included in an unbroken outer endodermis. The assumption would then be that in the case of *Platyzoma* there is no reasonable explanation of an inner endodermis unless the stele has been at some time possessed of stelar gaps by which the pith and cortex have been directly connected. *In thus assuming that the stele has been at some stage in its history on a more elaborate footing than at present, the supporters of the reduction theory would consider that the pericycle, phloëm, xylem, and inner parenchyma should normally be delimited from the ground-tissue of both cortex and pith by endodermal barriers.* To this it might reasonably be replied that the inner endodermis may have arisen when required in a growing intrastelar pith for purposes of intrastelar physiological control, the creation of the pith having rendered such a new endodermal formation necessary or advantageous. It may be asked, "From whence arose the outer endodermis?" The presumption seems to be that it was independently evolved when required for the delimitation of a primitive stele. And further, if the formation of outer endodermis antedated the evolution of inner endodermis, may it not be because the delimitation of the stele from the general ground-tissue antedated medullation? These are questions which cannot yet be definitely answered, but their bearing upon the present problem is obvious.

The conclusion to which this paper may be drawn is that in the case of *Platyzoma* the recorded ontogenetic facts would clearly allow of the tubular stele with independent outer and inner endodermis and only outer phloëm being the upgrade development from within of an original protostele. At the same time the reduction hypothesis would meantime suffer exclusion merely from lack of evidence in its favour. The stelar problem presented by *Platyzoma* cannot be solved until the "sporeling" stages have been fully investigated, and solenostely is proved or disproved.

#### SUMMARY.

The introduction to this paper consists of a summary of the facts of stelar structure already recorded for *Platyzoma*. These have been provided in succession by Dr POIRAULT, Mr BOODLE, and the present author. It is shown that in the materials so far examined the stele was an unbroken medullated cylinder devoid of either leaf-gaps or perforations. It was possessed of independent outer and inner endodermal sheaths, between which lay in centripetal succession pericycle, outer phloëm, xylem, and inner parenchyma. The included pith was entirely isolated within the conductive cylinder, having no ground-tissue connection with the cortex.

In leaf-trace-formation and -departure the inner endodermis was in no way involved, and no point existed where the stele was not entirely enclosed by an outer endodermis.

The theoretical statements which have been made regarding this stelar structure are then considered. They have been advanced by Dr POIRAULT, Dr JEFFREY, Mr BOODLE, and Mr TANSLEY. It is shown that in first suggesting that the pith of *Platyzoma* is the result of confluence and final isolation of a series of foliar sclerotic pockets, Dr POIRAULT imagined certain non-existing conditions as fulfilled in a Gleicheniaceous plant and merely contemplated through them a possible explanation for *Platyzoma*. He did not profess to support his interpretation by actual structural evidence from the plant itself. To Dr POIRAULT's conception of the stelar structure support has been given by Dr JEFFREY and Mr TANSLEY. The former has affirmed that the pith of *Platyzoma* is in reality of extrastelar origin, or is at least most reasonably interpreted as such, though as a result of stelar reduction it no longer communicates with the peripheral cortex. Mr TANSLEY has held that there is reason for considering the stele of *Platyzoma* as reduced from an original solenostele by loss of internal phloëm and leaf-gaps. Dr JEFFREY has further claimed to have observed nearly degenerate leaf-gaps in the stele. It is shown that in none of the materials so far examined is there structural evidence which can be reasonably advanced to support a belief in the present reduced state of the stele of *Platyzoma* or of its present or prior possession of foliar gaps. As an alternative interpretation of the stelar structure Mr BOODLE has suggested that the medullated stele of *Platyzoma* may possibly have been derived from a protostelic origin by the direct formation of an independent intrastelar pith and inner endodermis.

It is held by the present author that the evidence so far advanced is inadequate to allow of a confident opinion regarding the nature and origin of the medullated stele of *Platyzoma*. For while no evidence of the intrastelar origin of the pith and inner endodermis has emerged to support Mr BOODLE's suggestion, the reduction theory is not supported by the demonstration of cortical "intrusion" into the stele through stelar gaps, nor by the presence of stelar gaps and a solenostelic condition. The reduction hypothesis seems to stand upon the more comprehensive assumptions, but neither view can claim to be considered to indicate more than the undemonstrated possibilities.

A description of the stelar structure of a number of recently acquired incomplete specimens of *Platyzoma* follows. It is shown that in the majority of these the stelar-structure was identical in plan with that already described. Neither a solenostelic condition nor evidence of degenerate stelar gaps or inner phloëm was found. The investigation of these plants added nothing to our knowledge which materially alters or helps to solve the problem of the origin of the pith and the nature of the stele. But on the reduction hypothesis they might be considered evidence of the firm establishment of the reduced condition, while on the theory of

upgrade intrastelar differentiation they might be held to demonstrate how entirely intrastelar in nature as in location are the pith and inner endodermis.

On the other hand, a small—and possibly young—but incomplete specimen revealed some interesting features which are illustrated in the accompanying plates. It is shown that as its stele was followed forward from the broken base the pith and inner endodermis decreased until the latter was narrowed to a vanishing point and a medullated protostele was locally established (figs. 1-5). The pith again expanded and within it there arose *de novo* an inner endodermis, which, at first of irregular and indefinite construction, was subsequently definitely tubular (figs. 6-11). By disintegration of this wide tubular inner endodermis an irregular formation again arose within the pith, but when the latter had once more diminished the inner endodermis was an unbroken tube narrowing on a vanishing point (figs. 12-15). For at least the second time in the history of this plant a medullated protostele was established locally (fig. 16), and on subsequent re-expansion of the pith inner endodermis was again created *de novo*, and was subsequently maintained to the apex of the stem as an unbroken cylinder (figs. 17-25).

A study of the stelar differentiation showed that the xylem was roughly divisible into two concentric cylinders. The outer of these was differentiated first and was alone involved in supplying xylem to the traces. In it the order of differentiation was indefinite and no spiral stelar protoxylems were recognised. The inner cylinder showed more or less clearly a centripetal order of differentiation. Spiral protoxylems were occasionally found in the departing leaf-traces but were not continuous into the stele. The theoretical position of the stem-protoxylems is mesarch.

The new facts of stelar-structure having been recorded, their bearing on the stelar problem is considered. It is recognised that *Platyzoma* is at points protostelic, and may augment from within the stele itself an attenuated pith. In like manner it has been seen to develop an intrastelar inner endodermis. Among the results secured there is nothing which can reasonably be considered evidence in favour of the reduction theory unless it be that protostely recurs where small leaf-traces predominate.

On the other hand, the theory of upgrade internal differentiation has not been proved, though the general trend of the structural evidence might reasonably be considered in its favour.

It is considered that any one of three definite states may exist in the stele of a fern.

- (i) The original protostely may persist undisturbed throughout the entire ontogeny.
- (ii) The original protostely may be transformed at an early stage in the ontogeny once and for all into one or other of the more elaborate stelar states.
- (iii) The original protostely may recur in the ontogeny in ferns in which the advanced stelar state is not yet permanently established.

It is suggested that *Platyzoma* may provide an illustration of this third and apparently exceptional state in which the protostelic structure of the ancestry has not yet been definitely restricted to the "sporeling" stages but tends to persist in the mature organism. If this be so, the structural evidence discussed in these pages may indicate a reminiscence of the steps taken in the initial transformation of the ancestral protostele, namely, the growth of a pith within the stele itself, and the inclusion of the bulk of this intrastelar pith within an independent internal endodermis created *de novo*. If this view should prove to be correct when "sporeling" plants have been examined, and if parallels to it be found in the ontogeny of other primitive ferns, the establishment of foliar gaps either late or early in the ontogeny, but *subsequent to medullation*, may reasonably be regarded as merely a further step in stelar amplification by which the initially distinct cortex and pith are sooner or later directly connected. On such a view the present medullated conductive cylinder of *Platyzoma* would be regarded as the high-water mark of stelar amplification so far reached for this plant, neither inner phloëm nor stelar gaps having been evolved.

In conclusion, it is held that the recorded facts would clearly allow of the tubular medullated stele of *Platyzoma* being the result of upgrade development from within of an original protostele. Nevertheless, the stelar problem cannot be solved until the "sporeling" stages have been investigated and solenostely and reduction are proved or disproved.

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## DESCRIPTION OF FIGURES IN THE PLATES.

(All the figures are from the stem of *Platyzoa*.)

## PLATE I.

Fig. 1. Transverse section of the stele at the broken base of the small plant described in the text. The inner endodermis is a narrow though uninterrupted tube. ( $\times 50$ .)

Fig. 2. Transverse section of the stele at a point in advance of that represented in fig. 1. The inner endodermis has been narrowed down to a very slender tube, and scattered tracheides are in the surrounding parenchyma. ( $\times 50$ .)

Fig. 3. Transverse section of the stele at a point in advance of that represented in fig. 2. The inner endodermis has diminished until it is merely a small group of cells including no pith. ( $\times 50$ .)

Fig. 4. Transverse section of the stele at a point in advance of that represented in fig. 3. The inner endodermis has now vanished and a medullated protosteles has been formed locally. ( $\times 50$ .)

Fig. 5. Transverse section of the stele at a point in advance of that represented in fig. 4. An almost solid protosteles has been formed. ( $\times 50$ .)

Fig. 6. Transverse section of the stele at a point in advance of that represented in fig. 5. The pith has expanded within the parenchymatous xylem. ( $\times 50$ .)

Fig. 7. Transverse section of the stele at a point in advance of that represented in fig. 6. An irregular endodermal formation has arisen in the growing pith. ( $\times 50$ .)

Fig. 8. Transverse section of the stele at a point in advance of that represented in fig. 7. The irregular inner endodermal formation has been resolved into an irregular tube and an isolated group of endodermal cells. ( $\times 50$ .)

Fig. 9. Transverse section of the stele at a point in advance of that represented in fig. 8. The inner endodermal tube has been ruptured and involves a single chain of endodermal cells. A new tube and sheet of endodermal cells have arisen within the pith. ( $\times 50$ .)

## PLATE II.

Fig. 10. Transverse section of the stele at a point in advance of that represented in fig. 9. A wide though still incomplete inner endodermal tube is indicated and includes an isolated endodermal cell. ( $\times 50$ .)

Fig. 11. Transverse section of the stele at a point in advance of that represented in fig. 10. The inner endodermal-cylinder is almost completely differentiated. ( $\times 50$ .)

Fig. 12. Transverse section of the stele at a point in advance of that represented in fig. 11. The inner endodermal-cylinder has been disrupted and an irregular endodermal-formation has arisen. ( $\times 50$ .)

Fig. 13. Transverse section of the stele at a point in advance of that represented in fig. 12. The inner endodermal-formation has been resolved into an incomplete tube around a limited body of pith and an irregular group of endodermal cells. ( $\times 50$ .)

Fig. 14. Transverse section of the stele at a point in advance of that represented in fig. 13. The pith has been greatly diminished and the irregular inner endodermis has become a narrow though incomplete tube. ( $\times 50$ .)

Fig. 15. Transverse section of the stele at a point in advance of that represented in fig. 14. The pith has been drastically diminished and the inner endodermal tube has been tapered towards a vanishing point. ( $\times 50$ .)

Fig. 16. Transverse section of the stele at a point in advance of that represented in fig. 15. A medullated protostele has been established locally. ( $\times 50$ .)

Fig. 17. Transverse section of the stele at a point in advance of that represented in fig. 16. The pith has been augmented and within it a new endodermal-formation has arisen. ( $\times 50$ .)

Fig. 18. Transverse section of the stele at a point in advance of that represented in fig. 17. A complete inner endodermal tube has been formed, and part of the pith which it includes is sclerotic. ( $\times 50$ .)

PLATE III.

Fig. 19. Transverse section of the stele at a point in advance of that represented in fig. 18. The inner endodermal-cylinder has become locally narrow. ( $\times 50$ .)

Fig. 20. Transverse section of the stele at a point in advance of that represented in fig. 19. The inner endodermal-cylinder has again expanded. ( $\times 50$ .)

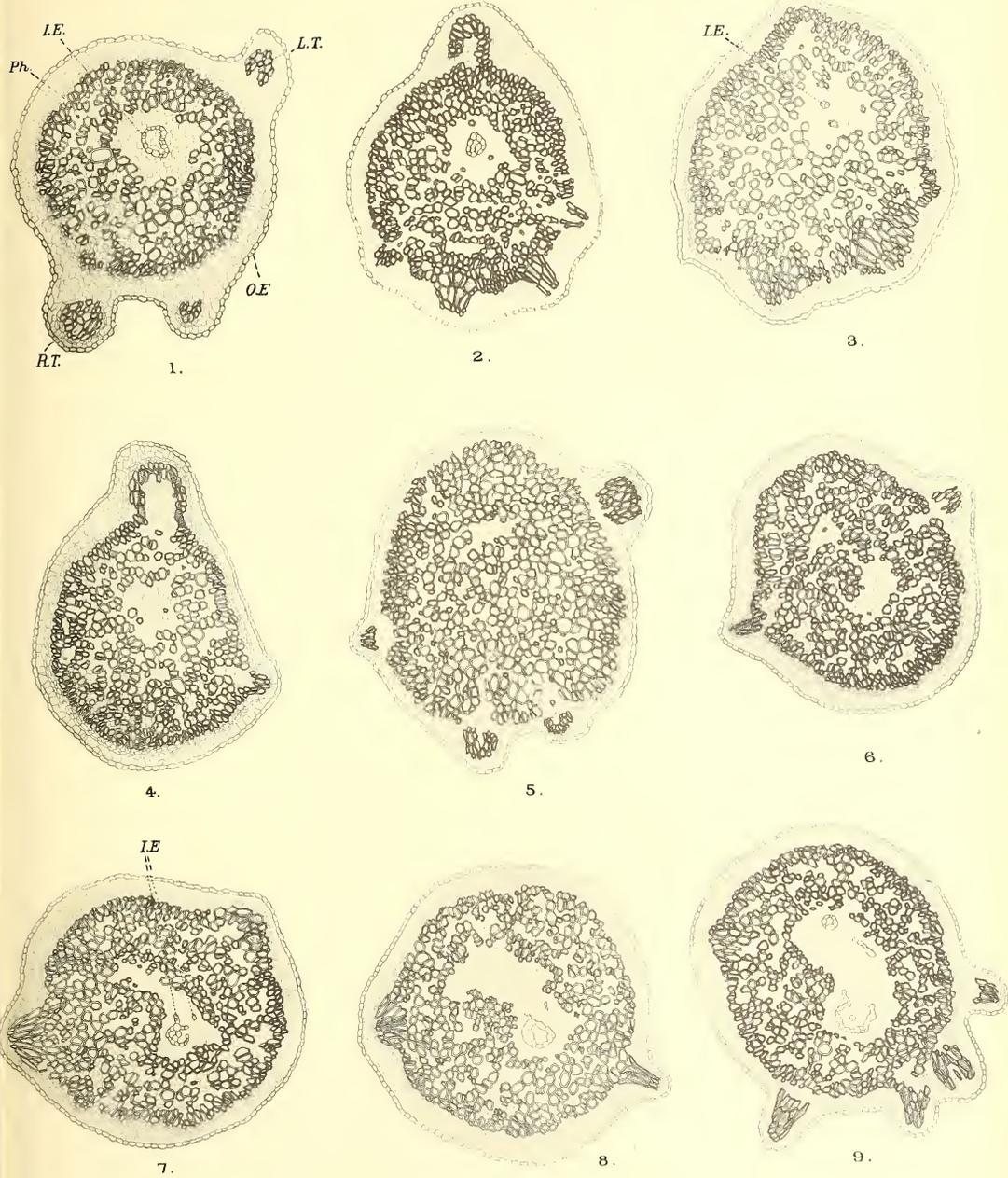
Figs. 21-25. A series of transverse sections of the stele at successive points in advance of that represented in fig. 20. Fig. 25 represents the undifferentiated stele just behind the growing apex of the stem, while figs. 24, 23, 22, 21 show successive steps in the stelar differentiation. ( $\times 50$ .)

Fig. 26. Transverse section of a portion of the vascular cylinder in a section lent by Dr SCOTT and Mr BOODLE. It represents a xylem-ray at the point of departure of a small leaf-trace. ( $\times 100$ .)

Fig. 27. Transverse section of a portion of the stele of *Platyzoma* to show the spiral protoxylem groups seen occasionally in the leaf-trace. ( $\times 100$ .)

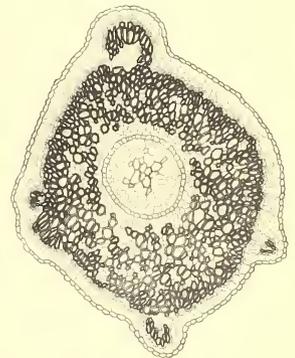
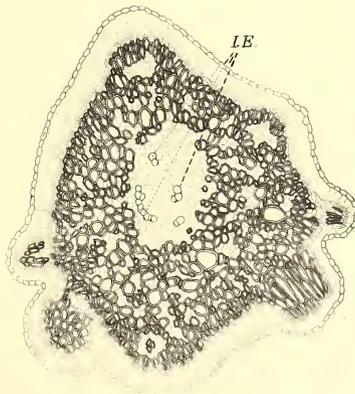
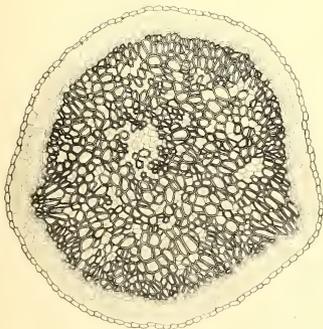
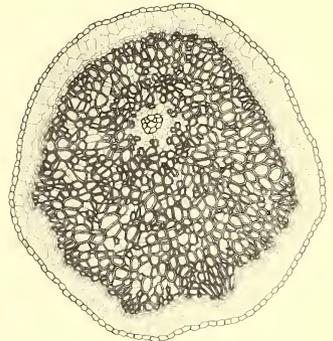
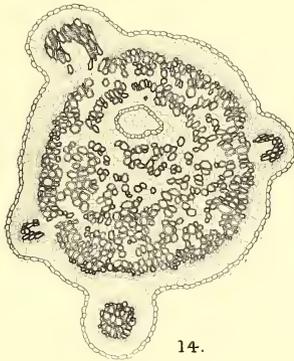
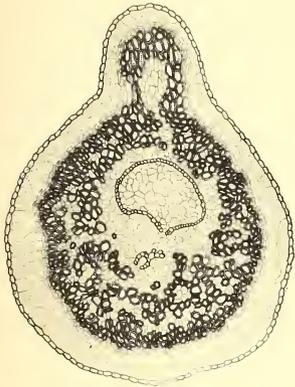
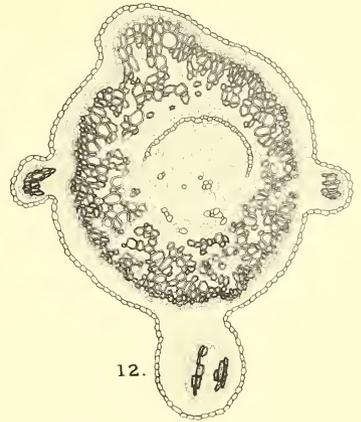
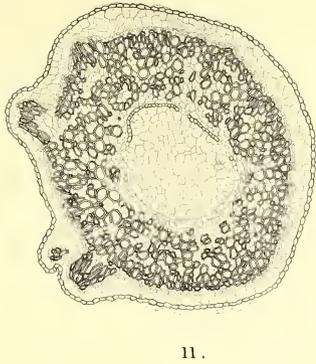
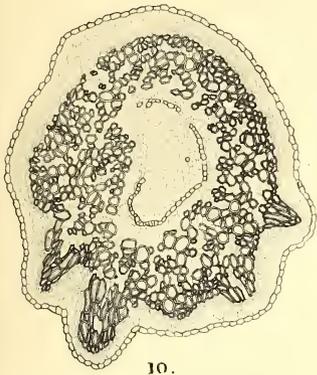


DR JOHN M<sup>C</sup>L. THOMPSON: PLATYZOMA MICROPHYLLUM R. BR. - PLATE I.



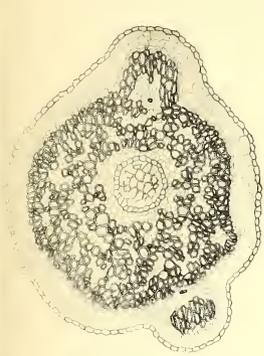


D<sup>r</sup> JOHN M<sup>c</sup>L. THOMPSON: PLATYZOMA MICROPHYLLUM, R.Br.—PLATE II.

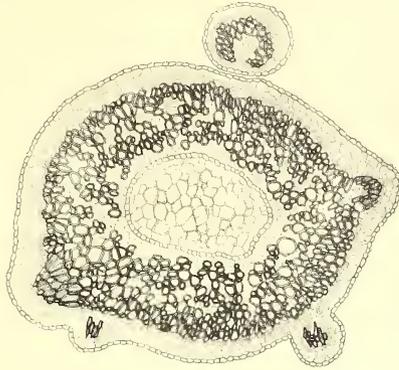




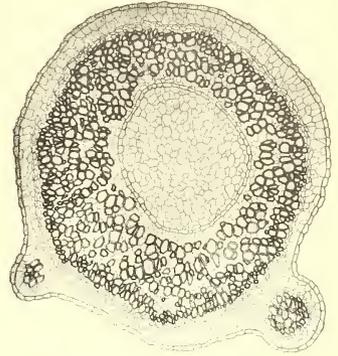
D<sup>r</sup> JOHN M<sup>c</sup>L. THOMPSON: PLATYZOMA MICROPHYLLUM. R. BR.—PLATE III.



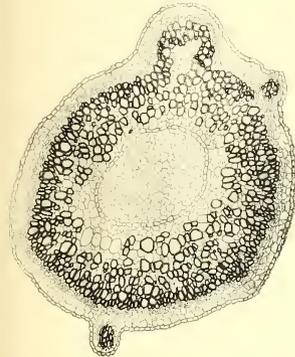
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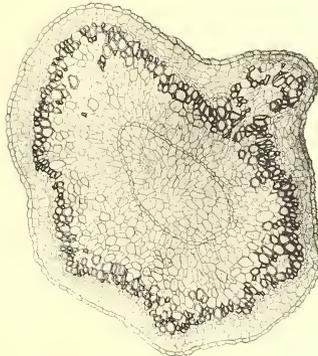
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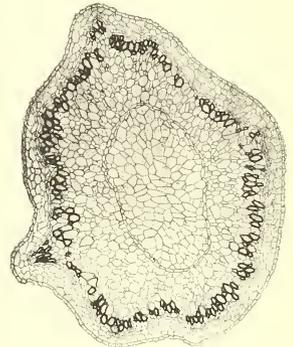
21.



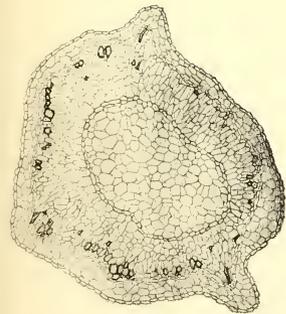
22.



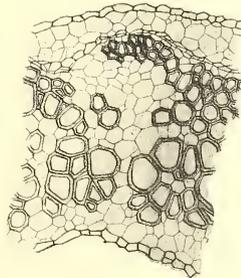
23.



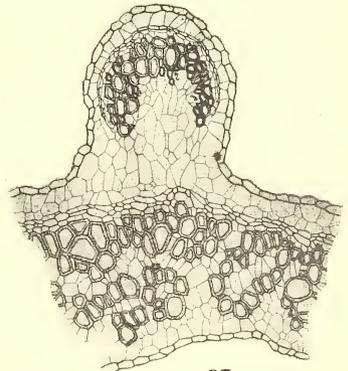
24.



25.



26.



27.



XXIII.—Amphicheiral Knots. By **Mary Gertrude Haseman**, Ph.D. *Communicated*  
by Dr C. G. KNOTT, *General Secretary*. (With One Plate.)

(MS. received May 20, 1918. Read November 4, 1918. Issued separately December 22, 1919.)

§ 1. THE INTRINSIC SYMBOL OF AN AMPHICHEIRAL.

The intrinsic symbol\* of an amphicheiral knot is based on the idea of the sequence of the crossings; it replaces each letter of the alphabetical symbol by a number equal to one-half of the number of crossings intervening before the next occurrence of that letter as the knot is traversed in a definite direction. Hence it is seen that two knots, which have the same intrinsic symbol, are identical. Since the same number of pairs of crossings must elapse before the next occurrence of corresponding crossings of two identical knots when the knots are traversed in a given direction, it is seen that the converse is true also. It may be necessary to consider the complementary intrinsic symbol in order to detect identical knots. For example, the two knots

- (1)           10 5 5 9 9 9 9 3 4 4 4 4 8 8 10 5 5 9 9 9 9 3 4 4 4 4 8 8  
              *a g b l c m d h i j f k g b h n e i j f k a l c m d n e*,
- (2)           3 5 5 9 9 9 9 10 4 4 4 4 8 8 3 5 5 9 9 9 9 10 4 4 4 4 8 8  
              *a g b l c m d a e j f k g b h n i e j f k h l c m d n i*,

are found to be identical since the intrinsic symbol of (1) coincides with the complementary symbol of (2). That they are identical may be verified by the fact that their compartment symbol is

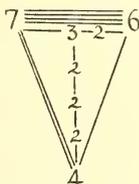


FIG. 1.

By an interchange of the two crossings, *a* and *h* in (2), it is seen that the two symbols may be made to coincide. So two amphicheiral knots are identical when their intrinsic symbols agree except for an interchange of complementary numbers.

The intrinsic symbol of an amphicheiral knot of the first order offers certain points of interest. An amphicheiral centre of an amphicheiral knot of order 1 is

\* M. G. HASEMAN, *Trans. Roy. Soc. Edin.*, vol. lii, p. 235.

defined as a mid-point of a lap of the thread so located that corresponding crossings occur at equal arcual distances when the knot is transversed along this thread in opposite directions from the point. Let the amphicheiral centre  $\phi_1$  be the mid-point of the lap of thread between the two corresponding crossings  $p$  and  $q$  of a knot with  $n$  crossings, and denote by  $\alpha_1, \beta_1$  the number of pairs of crossings which elapse before the next occurrence of  $p, q$  respectively as the knot is traversed from  $p$  to  $\phi_1$  through  $q$ . Hence  $n-1-\alpha_1, n-1-\beta_1$  will be the number of pairs of crossings which elapse before the next occurrence of the crossings  $p, q$  respectively as the knot is traversed from  $q$  to  $\phi_1$  through  $p$ . By the definition of an amphicheiral centre,  $\alpha_1 = n-1-\beta_1$  or  $\alpha_1 + \beta_1 = n-1$ . Similarly  $\alpha_j + \beta_j = n-1$ , where  $\alpha_j$  and  $\beta_j$  are two crossings of the intrinsic symbol at equal arcual distances from  $\phi_1$ . Thus an amphicheiral knot of the first order, as well as its pairs of amphicheiral centres, may be detected very easily from its intrinsic symbol. For example, the intrinsic symbol

$$\begin{array}{cccccccccccccccccccccccc} 4 & 4 & 4 & 8 & 4 & 8 & \cdot & 5 & 9 & 5 & 9 & 9 & 9 & 4 & \cdot & 9 & 4 & 4 & 4 & 8 & 4 & 8 & \cdot & 5 & 9 & 5 & 9 & 9 & 4 & \cdot & 9 \\ a & f & b & k & c & l & & d & n & e & a & f & b & g & & c & h & m & i & d & j & e & & k & g & l & h & m & i & n & & j \end{array}$$

exhibits one pair of amphicheiral centres between the crossings  $l, d$  and  $e, k$ , as well as a second pair between  $g, c$  and  $n, j$ .

On the other hand, from TAIT'S\* definition of an amphicheiral of the second order, it is seen that every crossing is separated from its correspondent by  $n-1$  pairs of crossings, and hence the first  $n$  numbers of the intrinsic symbol are identically equal to the remaining numbers, the sequence of numbers being the same. Accordingly the knot whose intrinsic symbol is shown in (1) on page 1 is an amphicheiral of the second order.

## § 2. A NEW CONSTRUCTION FOR THE AMPHICHEIRALS OF ORDER 1.

The intrinsic symbol for all of the amphicheiral knots of the first class of orders 1 and 2, as constructed by TAIT † is arranged in one of the two sequences stated above, whereas this is not the case for all of the amphicheirals of the second class of orders 1 and 2. However, in a census (M. G. HASEMAN, *Trans. Roy. Soc. Edin.*, vol. lii, p. 253) of the amphicheiral knots with twelve crossings, it is found that the form shown in fig. 3, which is obtained by the unsymmetrical distortion  $D_1^a D^c$  of the form shown in fig. 2, and belongs therefore to the second class, possesses the intrinsic symbol,

$$1 \ 7 \ 7 \ 10 \ 4 \ 4 \ 1 \ 7 \ 7 \ 10 \ 4 \ 4 \ 1 \ 7 \ 7 \ 10 \ 4 \ 4 \ 1 \ 7 \ 7 \ 10 \ 4 \ 4 ;$$

this classes it among the amphicheirals of the second order. But it is impossible to put this knot on the sphere so that corresponding compartments are opposite; that is to say, it cannot be constructed in the plane by means of a great circle and a pair of twin circuits. Hence it cannot belong to order 2 as defined by TAIT. ‡ It is

\* TAIT, *Trans. Roy. Soc. Edin.*, vol. xxxii, p. 497.

† *Ibid.*, Plate LXXIX.

‡ *Ibid.*, p. 497.

possible, however, to construct on the sphere one of the amphicheiral forms of the knot given in fig. 2 by means of a curve  $C_1$  in contact with a great circle at two diametrically opposite points,  $P_1, P_2$ , and of a curve  $C_2$  which is obtained as a reflection of  $C_1$  in the plane  $\pi_1$  of the great circle, followed by a second reflection in a plane  $\pi_2$  passed through the points  $P_1, P_2$  perpendicularly to the plane  $\pi_1$ . To secure this construction in the plane suppose  $c_1$ , which is the projection of the curve  $C_1$  in the plane  $\pi_1$ , to be the broken curve in fig. 4, with contacts at the diametral points  $p_1, p_2$ . The curve  $c_2$ , represented by the dotted curve, is the same curve as  $c_1$ , but drawn on the outside of the circle and reflected in the line  $p_1p_2$ . Now, imagine the curve  $c_2$  to be rotated through an angle of  $\frac{\pi}{4}$  to the right or left; the resulting knot, where the contacts are regarded as crossings, is found to be the knot shown in fig. 3.

The foregoing construction led me to seek for a similar construction in the plane of the amphicheirals of the first order with any number of crossings. Let the curve

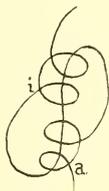


FIG. 2.

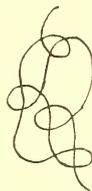


FIG. 3.

$c_1$  have  $\kappa$  contacts,  $2\iota$  intersections with the circle and  $\sigma$  self sections; and denote by  $c_2$  the same curve on the outside of the circle but reflected in a diameter passing through one of the contacts. Now, imagine  $c_2$  rotated through angles  $\frac{\pi}{\kappa}, \frac{2\pi}{\kappa}$ , etc., and the resulting curve is found to be an amphicheiral of order 1 with  $2(\kappa + 2\iota + \sigma)$  crossings. The curve  $c_2'$ , obtained by the reflection in the plane  $\pi_1$  of the great circle, ensures the desired correspondence of compartments; the reflection of the curve  $c_2'$  in the plane  $\pi_2$  does not alter the number of compartments, nor the number of laps of thread bounding each compartment; instead it interchanges corresponding adjacent compartments. For instance, suppose the two regions  $\rho_1, \rho_2$  by the first reflection to go into the two adjacent regions  $\rho_1', \rho_2'$  respectively. If, now, by the second reflection  $\rho_1$  becomes adjacent to  $\rho_2'$ , then  $\rho_2$  must become adjacent to  $\rho_1'$  by the same reflection. Since rotation through an angle merely adds one crossing to each of the regions which are in the relation of  $\rho_1, \rho_2'$ , then the desired correspondence of compartments remains unaltered. Further corresponding crossings occur at equal arcual distances from the mid-points of the lap of thread common to two corresponding compartments. Hence the knot is an amphicheiral of the first order.

It is possible to have the two curves  $C_1$  and  $C_2$  in their various positions intersect in  $\sigma'$  pairs of points, although it is not always possible to make corresponding laps of the thread intersect without introducing extra crossings. By this process I have succeeded in constructing all of the amphicheirals of order 1 with four, six, eight, and ten crossings (Nos. 1-21 in the Plate\*), and find the tenfold knot No. 21 in the Plate, omitted by TAIT in his census (*Trans. Roy. Soc. Edin.*, vol. xxxii, Plate LXXIX).

Likewise the knot No. 22 in the Plate has been omitted from my census (see *Trans. Roy. Soc. Edin.*, vol. lii, pp. 253-4) of the amphicheirals with twelve crossings. It is possible that this method will reveal other omissions. It is to be noted that the maximum number of contacts were used in the constructions of these amphicheirals,

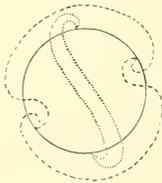


FIG. 4.

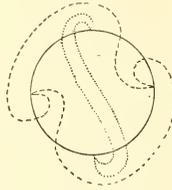


FIG. 5.

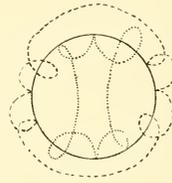


FIG. 6.

but I cannot say whether this is necessary in the construction of the knots with a greater number of crossings.

### § 3. SKEW AMPHICHEIRALS.

If, however, the curve  $c_2'$ , obtained by a single reflection in the plane  $\pi_1$ , is used instead of the curve  $C_2$ , there results upon rotation a knot which can be distorted into an amphicheiral of the first order—that is to say, it belongs to TAIT's second class. When the curve  $C_1$  is symmetrical about the line  $p_1p_2$ , the resulting knot is an amphicheiral of the first class of order 1, since then the curve  $c_2'$  is identical with the curve  $C_2$ .

In this construction there arise certain knots, called by me skew amphicheirals of the second order, which exhibit the amphicheiral symmetry in spite of the fact that they belong, by the above statement, to the second class of order 1. The intrinsic symbol of all such knots, as I have found, classes them with the amphicheirals of the first class of order 2, although corresponding regions are not opposite on the sphere. An example of a skew amphicheiral is shown in fig. 5; it is found to be identical with the knot in fig. 3. It is to be noted that in the knot shown in fig. 5 the curve  $c_2'$  possesses symmetry of such a nature that its relation to curve  $c_1$  is the same whether  $c_2'$  be rotated to the right or left.

\* The numbers at the lower right-hand corners are TAIT's numbers.

Another very good example (see fig. 6) of a skew amphicheiral is given by the symbol

1 3 3 22 1 8 8 22 20 20 15 15 1 3 3 22 1 8 8 22 20 20 15 15  
*a e b a c l d c e b f v g k h g i r j i k h l d*  
 1 3 3 22 1 8 8 22 20 20 15 15 1 3 3 22 1 8 8 22 20 20 15 15  
*m q n m o x p o q n r j s w t s u f v u w t x p.*

Because of the relation of the curve  $c_2'$  to the curve  $c_1$  the crossing  $a$  may correspond to either  $g$  or  $s$ ; likewise the crossing  $m$  may correspond to either  $g$  or  $s$ . Therefore we may expect not only the numbers in the last half of the sequence to be a repetition of those in the first half, but also the first half to consist of a repetition of a certain group of numbers; the number of repetitions will probably depend on the number of contacts.

The only skew amphicheirals, which I have found, may be obtained as the unsymmetrical distortions of an amphicheiral of the first class of order 1, and in view of the fact that the curve for knots with 4, 6, 8, 10, 12, 14 crossings seems to lead always to a knot which can be distorted into an amphicheiral of the first class of order 1, I am of the opinion that they do not constitute a distinct class, although it may be that they will form another class in the case of the knots with a greater number of crossings.

If, therefore, an amphicheiral knot is defined as one whose primary and secondary symbols are identical—that is to say, one whose intrinsic symbol belongs to one of the two arrangements mentioned on p. 598—it is seen that TAIT's classification given in *Trans. Roy. Soc. Edin.*, vol. xxxii, p. 499, is sufficient provided that it be admitted that an amphicheiral knot can belong to the first class of one order and to the second class of the other order.

§ 4. AMPHICHEIRAL KNOTS OF ORDER 2 WITH FOURTEEN CROSSINGS.

As has been shown by TAIT, *Trans. Roy. Soc. Edin.*, vol. xxxii, there are no amphicheiral knots of order 2 with 4, 6, 8, or 10 crossings. There are two knots\* of the second order with twelve crossings, both of which may be constructed on models involving one pair of contacts, although they appear among the knots which required a greater number of contacts. In a consideration of the maximum number of contacts necessary to construct the amphicheirals with  $n$  crossings I was led to construct the amphicheirals of the second order with fourteen crossings, of which there are ten in number, as shown in Nos. 23–32 in the Plate. Nine of these were constructed on models with one pair of contacts, whereas the tenth one, No. 32, required two or more pairs of contacts. Hence it will be necessary to pass to the amphicheirals with a greater number of crossings in order to determine the maximum number of contacts required.

An interesting amphicheiral is the form which is obtained by the single distor-

\* M. G. HASEMAN, *Trans. Roy. Soc. Edin.*, vol. lii, p. 254.

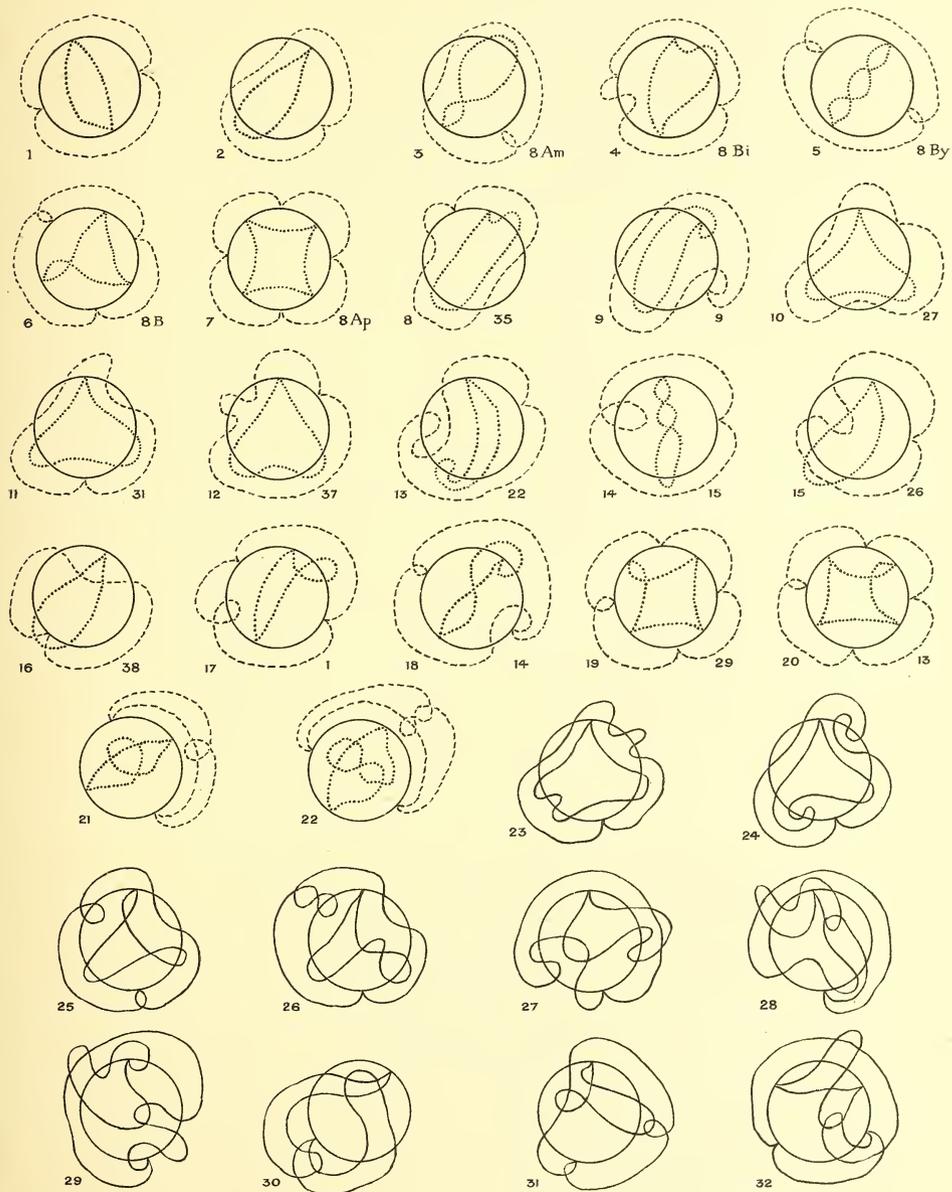
tion  $D_1$  of the amphicheiral of the second order with fourteen crossings, No. 25 in the Plate. Its intrinsic symbol

11 10 3 3 11 10 4 3 1 10 10 12 4 3 10 9 1 3 3 12 10 9 3 2 10 10 3 2

shows that it is an amphicheiral of the first class of order 1 with one pair of amphicheiral centres. This is an example of TAIT's supposed third class (*Trans. Roy. Soc. Edin.*, vol. xxxii, p. 499), which has the property of being changed into its own perversion by a single distortion, but, contrary to his idea, it must belong to the first class of order 1 and to the second class of order 2.

It is of interest to note that all of those amphicheirals which belong simultaneously to the first class of orders 1 and 2 exhibit two pairs of amphicheiral centres with the exception of one, which has fourteen pairs.

MARY G. HASEMAN: AMPHICHEIRAL KNOTS.





XXIV.—On Old Red Sandstone Plants showing Structure, from the Rhynie Chert Bed, Aberdeenshire. Part II. Additional Notes on *Rhynia Gwynne-Vaughani*, Kidston and Lang; with Descriptions of *Rhynia major*, n.sp., and *Hornea Lignieri*, n.g., n.sp. By R. Kidston, LL.D., F.R.S., and W. H. Lang, D.Sc., F.R.S., Barker Professor of Cryptogamic Botany in the University of Manchester. (With Ten Plates.)

(Read July 8, 1918. MS. received May 17, 1919. Issued separately January 20, 1920.)

#### INTRODUCTION.

In Part I\* a general account was given of the silicified peat-bed found at Rhynie, and one vascular plant was described in detail under the name of *Rhynia Gwynne-Vaughani*. Further study has shown that there are two species of *Rhynia* which we now distinguish as *Rhynia Gwynne-Vaughani* and *Rhynia major*. The account in Part I applies to both these species. Along with them there occurs a plant of similar grade of organisation to *Rhynia*, though quite distinct from that genus: this we name *Hornea Lignieri*. *Asteroxylon Mackiei*, on the other hand, which will be described in the next part, was a plant of larger size and much more complex morphology.

We are thus now able to establish the existence and main features of four archaic Vascular Cryptogams from the Rhynie bed. In the present paper additional notes on *R. Gwynne-Vaughani* are given, and *R. major* and *Hornea Lignieri* described in detail. In conclusion, the morphological bearings of the facts will be briefly considered.

Our former paper was based mainly on sections prepared from loose blocks of the chert, and partly from specimens collected from the chert bed *in situ*. The material for the present paper was mostly obtained in position in the chert bed, though a few loose blocks have yielded valuable information.

#### RHYNIA.

As mentioned above, two species of *Rhynia* have to be distinguished. Their similarity in organisation is so great that they are not always readily separated from one another, and in our former paper they were described together under the name *Rhynia Gwynne-Vaughani*. The second species, which we now separate as *Rhynia major*, is larger in all its parts, and differs from *R. Gwynne-Vaughani* in the absence of the hemispherical projections and adventitious branches from the stems, in the greater size of the stele and xylem strand, and in the much larger size of the sporangia and spores.

\* *Trans. Roy. Soc. Edin.*, vol. li, 1917, p. 761.

The difficulty of sharply distinguishing particular fragments of these two plants is in no way inconsistent with the opinion we have been led to form, that they are distinct but closely allied species. Their comparative study is assisted by certain beds or loose blocks containing the remains of only one or the other species. The difference in size of the two plants will be evident on comparing the block of chert represented of natural size in Pl. I, fig. 1, with the figs. 2 and 5 on Pl. II of our former paper. The peat in fig. 1 is composed of stems of *R. major*, many of which have a diameter of 5 mm., while the stems of *R. Gwynne-Vaughani* in figs. 2 and 5 are about 2 mm. in diameter.

Although we were dealing with mixed material of two species, which we now know separately, the description of the plant and its differentiation into rhizome, stems, and sporangia given in Part I holds good for both species of the genus *Rhynia*. It has only to be qualified by recognising the specific differences to be dealt with below. It will be convenient at this stage, however, to review the illustrations to our former paper and to indicate which belong to *R. Gwynne-Vaughani* and which to *R. major*.

All the figures on Pl. II are of *R. Gwynne-Vaughani*, as are also figs. 6-10 on Pl. III, fig. 20 and figs. 23-30 on Pl. V, all the figures on Pl. VI except fig. 37, and all the figures on Pls. VII and VIII. The sporangium in figs. 63 and 63A on Pl. IX is the only one figured that belongs to this species. Figs. 72-74 on Pl. X are small stems of this species. A survey of the figures named shows that the general habit and size of *R. Gwynne-Vaughani*, the external features of the stems, the details of structure of the stems, the hemispherical projections and the occurrence in their place of adventitious branches, and the sporangium were represented. The transverse section of a stem in Dr MACKIE'S paper,\* which was the first figure of *Rhynia* published, also belongs to this species.

To *R. major*, on the other hand, we now refer fig. 1 on Pl. I, showing a block of the chert with the stems of natural size; all the figures of rhizomes on Pl. IV (figs. 13-19), with the details in figs. 11 and 12 of the preceding plate; the large stems in figs. 21 and 22 † of Pl. V; the outer cortex and stoma in fig. 37 on Pl. VI; the large sporangia in figs. 62 and 64-69 on Pl. IX; the spores in figs. 70 and 71 of Pl. X; and the partially decayed stems in figs. 76-78 of the same plate.‡ Consideration of these figures will show that the rhizomes, stems, and sporangia of *R. major* were represented, though the detailed account of the structure of the stem is based on *R. Gwynne-Vaughani*. On the other hand, all the rhizomes described and figured in Part I are of *R. major*, and the description of the sporangium is mainly based on this species.

The rhizomes figured on Pl. IV of Part I all occurred in one block of silicified

\* *Trans. Edin. Geol. Soc.*, vol. x, 1913, pl. xxii, fig. 5.

† The magnification of figs. 21 and 22 on Pl. V of Pt. I was erroneously given as 20 diameters. These stems are magnified about 14 diameters.

‡ To complete this survey of the illustrations to Part I, it should be stated that the poorly preserved specimen in fig. 75 of Pl. X does not belong to *Rhynia*, but to *Asterocylon*.

peat, composed of partly decayed stems of *R. major*, with sporangia of that species, and were evidently preserved as they grew at one level of the peaty mass. The presumption is that they belong to *R. major* and not to *R. Gwynne-Vaughani*, no stems of which are found in this block. This conclusion, though confirmed by some details, would be difficult without the evidence afforded by association. Rhizomes of *R. major* have, however, now been met with in other blocks, and rhizomes of similar type, though smaller, which undoubtedly belong to *R. Gwynne-Vaughani* will be described below.

#### ADDITIONAL NOTES ON RHYNIA GWYNNE-VAUGHANI, Kidston and Lang.

(Pl. I.)

1917. *Rhynia Gwynne-Vaughani*, Kidston and Lang (*pars*), *Trans. Roy. Soc. Edin.*, vol. li, p. 764, pl. ii, figs. 2-5; pl. iii, figs. 6-10; pl. v, figs. 20, 23-30; pl. vi, figs. 31-36, 38-40; pl. vii, figs. 41-51; pl. viii, figs. 52-61; pl. ix, figs. 63-63A; pl. x, figs. 72-74.

Many of the features of *R. Gwynne-Vaughani* were sufficiently described and illustrated in Part I, and only some supplementary notes are required.

Since there is reason to regard all the rhizomes described in Part I as of *R. major*, a rhizome belonging to *R. Gwynne-Vaughani* is figured here (Pl. I, fig. 1). The rhizome, which is cut transversely, has given off laterally an ascending stem. This rhizome has a thin-walled epidermis, a slight but evident distinction between outer and inner cortex, and a small stele, the xylem of which consists of about four tracheides. Rhizoids extend downwards into the peat from the epidermis of the lower side of the rhizome. The ascending branch shows epidermis, cortex, phloem, and xylem; it agrees in size and structure with the typical stems of *R. Gwynne-Vaughani* making up the peat of this region of the bed. Comparison with the rhizomes of *R. major* in Part I will show the essential similarity in structure of this region of the plant in the two species, and the difference in size.

We have little to add to the description of the stem in Part I, which was based almost entirely on this species. It may, however, be pointed out that, while the small strand of xylem is often uniform and composed of similar tracheides, this is not always the case. In larger strands a distinction of smaller central tracheides surrounded by outer tracheides of greater diameter is evident. This distinction can be seen in figs. 41 and 45 on Pl. VII of Part I. Attention is directed to this character in *R. Gwynne-Vaughani*, since it will be found to hold regularly and strikingly for the steles of *R. major* and *Hornea Lignieri*.

In the peat, composed of numerous stems of *R. Gwynne-Vaughani*, a number of cases have been noticed in which stems have been cut in the neighbourhood of their tips. The most striking example is shown in Pl. I, figs. 2-4, and demonstrates the appearance of the growing point. Fig. 2 shows at *a*, among a group of typical stems of this species, one with its tip cut longitudinally. This tip is more highly magnified

in fig. 3. The meristematic tissue is composed of small cells filled with dense contents, which evidently represent the slightly contracted protoplasts. The elongation of the cells in the central region of the stem is apparent a short distance behind the actual apex. The cells of the growing point itself are isodiametric, and those of the outermost layers were evidently undergoing periclinal divisions. The whole appearance suggests a small celled meristem, but it is of course impossible to say whether an apical cell was present or not. The cuticle can be traced from the older contracted region of the branch over the growing point; it has become separated from the outermost layer of cells by a clear zone.

By the side of this undoubted apex, at *b* in fig. 2, is seen what we can only interpret as the extreme tip of another growing point which has been removed by a horizontal section and is thus viewed from above. The arrangement of the meristematic cells in this transverse section is shown more highly magnified in fig. 4. If this interpretation is correct, the specimen gives additional evidence as to the absence of any prominent initial cell.

In connection with the apical meristem, fig. 5 may be referred to. This longitudinal section, while not including the apex, shows a region situated close to it with the protoplasts almost filling the small cell cavities.

The only sporangium of *R. Gwynne-Vaughani* figured in Part I (Pl. IX, figs. 63, 63A) lay amongst characteristic stems of that species, and terminated a stem showing the distinctive vascular strand and tracheides. It contrasted with what we now know to be the sporangia of *R. major* by its much smaller size. It measured about 3 mm. in length by 1 mm. across. At the junction of stalk and sporangium in this specimen there is a constriction (Pl. I, fig. 6) to which we do not attach importance as indicating a natural feature. Above the constriction the epidermal cells assume the character of the sporangial wall. They are deeper than on the vegetative stem, but as seen in surface view at the top of the sporangium have the fusiform outline (Pl. I, fig. 7). The cell walls are moderately thickened and brown. Within the well-marked epidermis come some layers of thin-walled tissue, mostly perished, and only indicated towards the base of this sporangium. Bounding the empty cavity of the sporangium is the persistent layer which we have spoken of in Part I as the "tapetum." The nature of this layer in the sporangia of *Rhynia* will be further considered below under *R. major*.

A transverse section of a slightly larger sporangium is shown in fig. 8. The well-developed epidermal layer, the perished middle zone of the sporangial wall, and the persistent tapetal layer can be distinguished. The sporangial wall is about .2 mm. in thickness, and the width of the sporangium must have been slightly over 1.5 mm. There were no spores remaining in this sporangium, but another of similar size, and with an equally well differentiated wall (fig. 9), was filled with well-preserved spores. The tapetal layer in this specimen appears a number of cells deep, but this is probably to be explained by the section being oblique.

The sporangium represented in fig. 10 is peculiar in that the epidermal layer of its wall is not sharply distinguished from that of the stalk. A firm tapetal layer seems to be completely wanting, though the soft tissues of the wall are well preserved. This peculiar sporangium widened out gradually from the stalk without any constriction at the base. The sporangial cavity is partly filled with mature spores.

Another small sporangium (fig. 11) was even more remarkable. The group of spores, still arranged in tetrads, is surrounded by a thick wall, which has neither a definite tapetal layer nor a characteristic thick-walled epidermis. The ill-preserved epidermis is bounded by a cuticle which is ridged like that of adjacent vegetative stems of *R. Gwynne-Vaughani* (cf. Part I, Pl. VI, figs. 31, 36, p. 769).

The two sporangia last described, which clearly belong to *R. Gwynne-Vaughani*, suggest a less differentiated condition in which spores were formed within the end of a stem without this being modified into a definite sporangium. It is of interest to find this type of sporangium co-existing in the same species with a more specialised type, provided with a tapetal layer and a specially constructed and thickened epidermal layer. There is no evidence, however, that any of the sporangia of this plant had a definite dehiscence.

The spores of *R. Gwynne-Vaughani* in the sporangium in fig. 11 were still associated in tetrads (fig. 12). Other mature spores from the sporangium in fig. 9 are represented in fig. 13. The fully mature but not shed spores of this species measure about 40  $\mu$  in diameter.

#### RHYNIA MAJOR, n.sp. (Pls. II and III.)

1917. *Rhynia Gwynne-Vaughani*, Kidston and Lang (*pars*), *Trans. Roy. Soc. Edin.*, vol. li, pl. i, fig. 1; pl. iii, figs. 11-12; pl. iv, figs. 13-19; pl. v, figs. 21-22; pl. vi, fig. 37; pl. ix, figs. 62, 64-69; pl. x, figs. 70, 71, 76-78.

The figures quoted above, and the descriptions in Part I based upon them, give the structure of all the regions of the plant—rhizomes, stems, sporangia—of *R. major*. It has been already pointed out that the differences distinguishing this species from *R. Gwynne-Vaughani* are mainly those of size and of minor details. It is necessary to consider the new species a little more fully, however, in order to bring out clearly the nature of these differences.

The remains of *R. major* so far found do not give any such picture of the habit of the plant as a whole as the specimen figured in Part I, Pl. II, fig. 5 did for *R. Gwynne-Vaughani*. The greater diameter of the stems, as shown in Pl. I of Part I, suggests that *R. major* was a larger plant throughout, and this is supported by the large size of the sporangia. We have, however, no direct evidence of the height this species attained.

We have nothing to add to the description of the rhizomes of *R. major* given in Part I, except to record the occurrence of similar though less perfect examples,

also associated with the typical stems of this species, in some specimens of the silicified peat collected from the section exposed *in situ*.

The stems of *R. major* must be more fully described, since the description of the stem of *Rhynia* in Part I was almost entirely based on specimens of *R. Gwynne-Vaughani*.

As regards size, the examination of large numbers of sections of stems has shown that in *R. major* a diameter of 5-6 mm. was often attained (Pl. II, figs. 14, 19). Finer branches, probably from the upper region of the plant, are met with down to a diameter of 1.5 mm. or less (fig. 15). These measurements contrast with those of *R. Gwynne-Vaughani*, in which the usual diameter of larger stems is about 2 mm., though a thickness of over 3 mm. is sometimes attained, while the finer stems or branches may be less than 1 mm. in diameter.

On Pl. V of Part I two transverse sections of *R. major* were figured in figs. 21 and 22. Large as they appear in comparison with the other stems on the same plate, the difference is in reality greater, since their magnification should have been given as  $\times 14$  instead of  $\times 20$ . A true comparison with the stems of *R. Gwynne-Vaughani*, magnified 20 diameters, in Part I, Pl. V, figs. 23-29, is afforded by the accompanying figs. 14, 19, 17, and 15 on Pl. II of this memoir.

A general view of a portion of the silicified peat composed of large stems and sporangia of *R. major* is given at a lower magnification ( $\times 7$ ) in Pl. III, fig. 25. The stems shown in figs. 18 and 21 are magnified 14 diameters.

All these figures show how closely the stem of *R. major* agrees in general construction with that of *R. Gwynne-Vaughani*.\* As is best shown in the well-preserved stem in fig. 14, there is a clear differentiation into epidermis (*ep.*), outer cortex (*o.c.*), inner cortex (*i.c.*), phloem (*ph.*), and xylem (*x.*). A difference that may be at once emphasised is the absence of the hemispherical projections which are such a striking feature of many stems of *R. Gwynne-Vaughani*. In the large number of sections of *R. major* examined no trace either of hemispherical projections or of the adventitious branches corresponding in place of origin to them has been seen.

The epidermis had the outer walls thickened and covered with a well-marked cuticle. It appears smooth, and no ridges have been observed on the epidermal cells. Stomata were sparingly present as in *R. Gwynne-Vaughani*. The outer cortex, two or three cells deep, was evidently a mechanically important hypoderma in the larger stems. Within it came the wide inner cortex, the outer cells of which, when well preserved, often have the dark contents common in the same position in *R. Gwynne-Vaughani* (fig. 14). The outer cortex was interrupted beneath the stomata, as is shown in figs. 14 and 18 and in Part I, Pl. VI, fig. 37. In the large stems the outer cortex was very resistant to decay, while the wide inner cortex often broke down (figs. 25, 19, 18).

\* This is also brought out in comparing figs. 21 and 22 with the other figures on Pl. V of Pt. I.

The stele, which is clearly marked off from the inner cortex, though no special boundary line is present, has a wide clear zone of phloem surrounding the central solid strand of xylem. Even in the smallest stems of *R. major* (fig. 15) the stele is relatively large as compared with *R. Gwynne-Vaughani*.

The cells of the phloem are thin-walled, and as seen in transverse section (fig. 16) fit closely together. The intercellular spaces present in the inner cortex, when this is well preserved, cease on passing to the phloem. In longitudinal sections (figs. 17 and 20) the cells of the phloem are seen to be thin-walled and elongated, resembling the same tissue in *R. Gwynne-Vaughani*.

The xylem consists of far more numerous tracheides than in most steles of *R. Gwynne-Vaughani*. A distinction, such as was occasionally found in the latter plant, is here regularly present between the central and peripheral tracheides. The inner tracheides are much smaller than the outer ones, and have thinner walls (figs. 22, 16A). Although the xylem appears beautifully clear in many transverse sections, no satisfactory indication of the thickening of the tracheide walls is shown in any of the longitudinal or oblique sections as yet examined. Everything points to the walls having been thickened, but the thickening seems to have readily perished, and practically all the material of the plant had undergone decay to this extent at least. There is sometimes an appearance of porose thickening, but this often fills up the cavity, and from the examination of many specimens we are convinced that this appearance is due to an alteration of the original thickening, and that it would not be wise at present to attach any weight to it.\*

While, as stated above, no adventitious branches have been met with in *R. major*, the stems of this plant showed equal or dichotomous branching. An example is seen in Pl. III, fig. 21, at *a*, where two steles of the same size are present in the one cortex.

A number of sporangia of *R. major* were figured in our previous paper (Part I, Pl. IX, figs. 62, 64-69), and the description of the sporangium there given is based on them, and applies to this species. The figures on this plate show how much larger the sporangia of *R. major* were than those of *R. Gwynne-Vaughani*. There is some range in size of the sporangia of *R. major*, and still larger examples than any described in Part I have since been met with. Thus the sporangium on Pl. III, fig. 24, was nearly 4 mm. in diameter. Its wall was well preserved, and showed the vertically extended, thickened epidermal cells (*ep.*), the zone of thin-walled tissue (*m.l.*), and the "tapetal" layer (*tap.*) around the large cavity filled with spores.† The sporangium in Pl. III, fig. 23, may have been slightly larger, since the wall is broken and overlapped at *a*; only the epidermal layer enclosing the spores is preserved. It seems clear that the sporangia of *R. major* attained a length of more than 12 mm., a diameter of more than 4 mm., and a thickness of wall of 3-4 mm.

\* The decayed steles in Pt. I (Pl. X, figs. 76-78) belong to *R. major*, and the comparison there made with Dawson's figure of *Psilophyton* must be modified in so far as the outer dark zone in our specimens is derived from the outer xylem and not as suggested from the altered phloem.

† Cf. Pt. I, Pl. IX, fig. 67.

The spores (Pl. III, fig. 26) were about  $65\ \mu$  in diameter. The difference in size from the spores of *R. Gwynne-Vaughani* was constant in all the sporangia of the two species so far studied.

The remarkable and very persistent layer of cells which lines the cavity of the sporangium in both species of *Rhynia* has been referred to throughout as the "tapetum." Its position corresponds to that of a persistent tapetal layer, but it shows peculiarities which call for special remark. When best preserved it is seen to be a layer of somewhat flattened, elongated cells, the *walls* of which remain bounding the empty-looking cell cavities. It suggests to our minds a relatively rigid tissue, and is perhaps best compared with the sheath of tracheidal cells which has been described in some other fossil sporangia.\* The appearance of the walls of these "tapetal" cells in *Rhynia* is quite consistent with their being of tracheidal nature, though the preservation does not allow of any special thickening being recognised.

#### DIAGNOSIS.

The recognition of two species of *Rhynia* necessitates some modification of the generic characters and a differential description of the species.

#### *Rhynia.*

Plant gregarious, rootless and leafless, consisting of subterranean rhizomes attached by unicellular rhizoids, and erect, dichotomously branched, cylindrical aerial stems. Stomata present. Stele consisting of a zone of phloem surrounding a strand of tracheides. Sporangia cylindrical, without columella, terminal on aerial stems. Homosporous. Spores with cuticularised wall, developed in tetrads.

#### *Rhynia Gwynne-Vaughani.*

Aerial stems tapering upwards, probably about 20 cm. high, and ranging in thickness from 3 mm. to under 1 mm. Small hemispherical protuberances of superficial tissues of the stem occur, and sometimes, in place of them, adventitious branches, the stele of the branch not being continuous with that of the main stem. Xylem strand of stele slender, only sometimes showing a distinction of smaller central and larger peripheral tracheides. Tracheides with broad annular thickening. Sporangia about 3 mm. long and 1.5 mm. in diameter. Sporangial wall about .2 mm. thick. Spores about  $40\ \mu$  in diameter.

*Locality.*—Muir of Rhynie, Aberdeenshire.

*Horizon.*—Old Red Sandstone (not younger than the Middle Division of the Old Red Sandstone of Scotland).

\* F. W. OLIVER, "On a Vascular Sporangium from the Stephanian of Grand Croix," *New Phytologist*, vol. i, p. 60.

*Rhynia major.*

Plant larger in all its parts than *R. Gwynne-Vaughani*. Aerial stems tapering upwards, and ranging in thickness from 6 mm. to 1.5 mm. or less. No hemispherical projections or adventitious lateral branches. Stele large, xylem strand of numerous tracheides differentiated as smaller central and larger peripheral tracheides. Sporangia reaching a length of 12 mm. and a diameter of 4 mm. Sporangial wall about .3-.4 mm. thick. Spores about 65  $\mu$  in diameter.

*Locality*.—Muir of Rhynie, Aberdeenshire.

*Horizon*.—Old Red Sandstone (not younger than the Middle Division of the Old Red Sandstone of Scotland).

## HORNEA LIGNIERI, n.sp. (Plates IV-X.)

Another vascular plant from the Rhynie peat-bed agreed in general build with *Rhynia*, but differed in the sporangia having a columella of sterile tissue, around and above which the dome-shaped spore-sac extends. We regard it as a distinct, though allied, genus, and have named it after Dr Horne, to whose energy and interest the successful discovery of the Rhynie peat-bed *in situ* is largely due. The specific name has been given in reference to the acute morphological speculations of the late Professor LIGNIER, some of which gain confirmation and reality from the discovery of these simple types of Vascular Cryptogams.

The remains of *Hornea* occur in considerable quantity, at places forming an almost pure peat and elsewhere mixed with the other plants of the Rhynie deposit. The preservation is not quite so good as in the case of *Rhynia* and *Asteroxylon*, but shows all the essential structural features.

*Hornea Lignieri* resembled *Rhynia* in being a rootless and leafless plant, differentiated into rhizome, dichotomously branched cylindrical stems, and terminal sporangia. The continuity of these parts has been established. From the lobed tuberous rhizome, which was probably subterranean but might have been only partly embedded in the soil, a number of cylindrical stems arose separately. These bore no appendages, nor did they have hemispherical projections or lateral branches. They were from about 2 mm. to slightly under 1 mm. in diameter, and branched dichotomously. This occurs in the larger stems, but was probably more frequently repeated in the upper region of the plant, the stems diminishing in thickness as they subdivided. The sporangia terminated stems of various diameters, and show a corresponding range in size. The transformation of the end of a stem into a sporangium often affected a nascent dichotomy, the branching being then evident in the construction of the columellate sporangium.

The rhizome, stems, and sporangia may now be described in detail.

*Rhizome.* (Plates IV-VI.)

The rhizome of *Hornea* was of a different type from that of *Rhynia*, as will be evident from figs. 27 and 28 on Pl. IV. It had no vascular strand of its own, but was a lobed parenchymatous body of considerable size, from which arose stems, each provided with a central stele. The stele of each stem ended separately and blindly below in the parenchymatous tissue of the rhizome (figs. 35 and 38). Numerous long rhizoids attached the rhizome to the peat. From its resemblance to the protocorm of the young plants of some species of *Lycopodium*, this type of rhizome may be distinguished as protocormous from the stem-like rhizome of *Rhynia*. The largest rhizome met with is represented at a low magnification ( $\times 7\frac{1}{2}$ ) in fig. 31. It is branched, and at first sight appears of a different type, not being evidently lobed. It is, however, characteristic that no vascular system proper to the rhizome is seen. Comparison with the next section of the series showed that a number of stems arose from this rhizome, the plane of section in fig. 31 passing horizontally through the rhizome below the bases of the steles of these stems.

The general structure of the rhizome is shown in the vertical section in fig. 29. The plane of section just misses the stem, and the rhizome appears as a massive, somewhat flattened body, about 8 mm. across by 2 mm. thick. It is composed of thin-walled parenchymatous tissue, between the cells of which are small intercellular spaces.\* Towards the periphery the cells are somewhat smaller, and tend to be arranged in rows vertical to the surface, giving the appearance of an ill-defined outer cortex. The superficial layer constitutes a rather ill-defined epidermis, the small cells of which on the lower side of the rhizome bear the long rhizoids.

The rhizoids, which are visible in a number of the illustrations (figs. 29, 30, and 38), are non-septate, and each is a protrusion of the middle portion of the outer wall of an epidermal cell, from the cavity of which the rhizoid is not separated by a wall. Fig. 30 shows the rhizoid-bearing surface in vertical section, while in fig. 32 the surface is cut tangentially. Fig. 33 is a more general view of the latter section, and shows the long rhizoids extending from the small-celled epidermis.

The structure of all the rhizomes shown on Pls. IV, V, VI corresponds to that described above, some showing particular features more clearly. A number of them show the lobed form of the rhizome (figs. 27, 28, 35). In this connection the specimen in fig. 34 is of interest. A rhizome with a stem has apparently been cut obliquely, and two adventitious lateral growths had evidently developed from the superficial tissues as small protocormous rhizomes. The one shown in the figure bears rhizoids at *rh*.

No vascular elements were present in the section of the rhizome in fig. 29, though some of the internal cells have peculiar brown walls, and in their neighbourhood the

\* The question whether the fungal hyphae which occur in the intercellular spaces of the rhizome are to be regarded as saprophytic or mycorrhizic will be considered in a later paper when dealing with the fungi occurring in the Rhynian peat. Their frequent presence must, however, be mentioned here.

section was just touching the edge of the base of a stem-stele. The stems attached to the protocormous rhizomes in most of the specimens figured show their steles at some point or other.

The characteristic base of the vascular strand of a stem springing from a rhizome is best seen when the section is truly vertical to the rhizome and follows the median plane of the stem (figs. 35-38). The best specimen is that shown in figs. 35 and 36, the other two specimens serving to confirm it. As fig. 35 shows, one lobe of a rhizome has been cut vertically, and the section follows in an accurately longitudinal direction the stele of the stem arising from the lobe; the cortex has decayed from the further part of the stele as it lies in the peat. The rhizome shows the structure already described, and bore rhizoids below. While there is no vascular tissue in the rhizome itself, the stele of the stem when traced downwards into the upper part of the rhizome (figs. 35, 36) ends in connection with a brown-celled tissue without tracheidal thickenings. The inverted cup-shape of this mass of tissue is characteristic, though not often so favourably shown as in this specimen; it is seen also in figs. 37 and 38. It explains the frequent occurrence of patches of brown tissue in sections of rhizomes (*cf.* figs. 29 and 31).

#### *Stem.* (Plates VII and VIII.)

The basal regions of the stems attached to the rhizomes described above were often more or less decayed, but were sometimes well preserved. Portions of both the upper and lower regions of similar stems in various stages of decay make up the peat. A group of the best-preserved specimens is shown in fig. 39, some being cut in transverse and one in longitudinal section. The general similarity in structure to the stem of *Rhynia* will be evident, though the preservation is not so good in the material of *Hornea* yet examined. The well-defined cuticle and thickened epidermal wall, the broad cortex, and the stele with a zone of phloem surrounding the rather stout central strand of xylem, are distinguishable in fig. 39. The transverse section of a small stem from the upper region of the plant in fig. 40 may be compared with this. The corresponding regions are shown in longitudinal section in fig. 41.

The tissues may now be described in greater detail, starting from the outside (figs. 40 and 41). There was a well-marked cuticle. The epidermis had its outer walls somewhat thickened, but otherwise did not differ much from the underlying cortical cells. No stomata have been observed, but owing to the state of preservation of most of the material much weight cannot be attached to this negative result. The cortical tissues cannot be sharply distinguished into outer and inner cortex, though the cells diminish in diameter on passing inwards. The cortical cells are somewhat elongated, and have transverse end walls (fig. 41).

Within the cortex and immediately around the xylem was a zone of thin-walled elements which readily collapsed. This zone represents the phloem (figs. 42 and 43). It often has a peculiar appearance, as if the cells were thickened at the angles or small

intercellular spaces were present there (figs. 42, 43, 50, 51). In the more decayed stems the phloem may or may not be recognisable. It seems to have been less characteristically developed at the lower part of the stele near its insertion into the rhizome. All that can be said regarding the phloem in longitudinal section is that it consisted of narrower and more elongated elements than the cortex.

The xylem formed a centrally situated, solid strand of tracheides. It exhibits a considerable range in diameter, probably in relation to the regions of the stem-system of the plant. A xylem strand of moderate size is shown in transverse section in fig. 47, and others of larger size at the same magnification in figs. 45 and 48, with which fig. 46 can be compared. The xylem is shown more highly magnified in figs. 50 and 51. A distinction between narrower central, and wider peripheral tracheides is a constant feature. This holds for the steles of moderate diameter near to the rhizome, for the steles of large diameter, which we presume came from a region between this and the finer branches, and for the finer branches themselves. There are no thin-walled cells mixed with the tracheides, but the central xylem often appears broken down within a ring of peripheral xylem composed of wider and intact elements (figs. 43, 45, 46, 48). When such steles are cut longitudinally this appearance is seen to be due to repeated transverse breaks or interruptions of the core of central xylem, the tracheides of the peripheral xylem remaining continuous (fig. 49).

The thickenings on the tracheide walls have in most cases disappeared owing to the decayed condition of the stems. They are often best shown in the region of the stele near to the rhizome. In favourable specimens there is a distinct thickening of narrow bands forming irregularly connected rings or a spiral (figs. 52 and 53). As the extreme base of the stele in the rhizome is reached, the zone of phloem disappears and the tracheides become shorter and wider (fig. 54) and pass gradually into the brown-celled tissue at the base of the stele.

The stems of *Hornea* branched dichotomously, and sometimes show the stele dividing (figs. 55 and 56), or two equal steles enclosed in the same cortex (figs. 42 and 57). From the frequency with which it is met with in smaller stems, this dichotomous branching was probably most marked in the upper region of the plant.

#### *Sporangium.* (Plates IX-X.)

Sporangia of a remarkable type occur associated with the remains of the vegetative organs of *Hornea*, especially with the finer branching stems. The proof that they belong to this plant is afforded by sporangia terminating stems with the structure described above (figs. 58, 60, 61).

The general construction of the sporangium will be evident from the longitudinal sections in figs. 58-60, and the transverse sections in figs. 63 and 64. As these show, the sporangial cavity was enclosed by a fairly thick wall, and had a sterile column of tissue projecting so far from its base that the actual cavity is dome-shaped. The resemblance to the columella of some bryophytic sporogonia is so great as to

make it convenient to use the name *columella* for the sterile projection in *Hornea*. The cavity is filled by the numerous spores with cuticularised walls.

The sporangia evidently arose by the transformation of the tips of certain branches of the plant. When the apex was simple, a single sporangium (such as that shown in fig. 58 to the right, and in fig. 64) resulted. When, however, the apex was in a more or less advanced stage of division, this is reflected in the subdivision of the sporangium and the lobing or branching of the *columella*, as shown in fig. 58 to the left, and in fig. 63.

The stalk of the sporangium is thus simply an ordinary branch of the plant. It shows the same structure as the stem, with epidermis, cortex, and stele more or less well preserved. Stalks bearing sporangia and showing the position of the stele are represented in figs. 58 and 60. The size of the sporangium differs according to the size of the stem bearing it. Thus the sporangium in fig. 58 is about 2 mm. long by slightly over 1 mm. broad, while that in fig. 64 is about 2 mm. in diameter.

The wall of the sporangium was of considerable thickness (about '25 mm.), and its tissues, like those of the stems, are usually imperfectly preserved. An epidermal layer, a middle zone consisting of a number of layers of thin-walled cells, and a more resistant tapetal layer can be distinguished (figs. 65 and 67), as in the case of the sporangium of *Rhynia*. The wall shows irregularities in outline or projecting processes which do not seem to be wholly accounted for by accidental contraction. A common appearance is the flattening or broadening of the tip of the sporangium, as shown in figs. 58 and 59.

The epidermal layer of the sporangium is, at least in some cases, more marked than that of the vegetative stems. It is bounded by a cuticle, and has the outer walls of the cells thickened, the thickening extending inwards on the lateral walls. No indication of any place of dehiscence has been seen even in complete transverse sections. The structure of the epidermis is seen in figs. 67 and 68, while that of the wall as a whole is well shown in fig. 65. Below the epidermis comes a zone of some six layers of small thin-walled cells; this is usually badly preserved. The innermost layer of the wall is the persistent "tapetum," which is continuous over the *columella* and thus forms a complete lining to the sporangial cavity. The tapetal cells are well shown in fig. 70. Their walls are dark, and give the impression of having been rigid, as in the case of the corresponding layer in the sporangium of *Rhynia*. No indication of tracheidal thickening of these cells has been met with.

The *columella* (fig. 69) is composed of narrow, elongated, thin-walled cells which give the tissue, as usually preserved, a peculiar fibrous appearance. Though corresponding in position to a continuation of the stele of the stalk, it exhibits no agreement in histological structure with the central region of this, but resembles rather the phloem of the stele. The specimen shown in fig. 62 shows that the *columella* is directly continuous with the phloem of the stalk.

The spores are often met with still associated in tetrads (fig. 71), while in other

cases they have become isolated in the sporangial cavity (fig. 72). They measure about  $50\ \mu$  in greatest diameter. Spores are also found distributed through the peaty matrix in which the plant is embedded.

#### DIAGNOSIS.

*Hornea*, Kidston and Lang, n.g.

Plant rootless and leafless. Stems arising from protocorm-like rhizomes, dichotomously branched. Sporangia terminal on ultimate branches, with a sterile columella projecting from the base into the sporangial cavity, and cuticularised spores developed in tetrads.

*Hornea Lignieri*, Kidston and Lang, n.sp.

Plant small, consisting of a lobed rhizome from which arise stems which branch dichotomously and range from 2 mm. in diameter downwards. Stele of stem with a zone of phloem surrounding the xylem composed of small central and wider peripheral tracheides. Sporangia cylindrical, terminal on branches, indehiscent, with thick wall composed of thickened epidermis, thin-walled tissue, and persistent tapetal layer. Sterile columella composed of thin-walled elongated cells extending from base to near top of sporangium. Homosporous. Spores about  $50\ \mu$  in diameter.

*Locality*.—Muir of Rhynie, Aberdeenshire.

*Horizon*.—Old Red Sandstone (not younger than the Middle Division of the Old Red Sandstone of Scotland).

#### CLASSIFICATION OF RHYNIA AND HORNEA.

*Rhynia* and *Hornea*, while distinguished generically, agree so closely in the simplicity of their organisation that they must be regarded as genera of the same Family. For this Family we suggest the name Rhyniaceæ.

It is characterised by the plants being rootless and leafless and composed of rhizomes which bear rhizoids, branched aerial stems, and terminal sporangia. The vascular system is correspondingly simple, the central stele having a cylindrical strand of xylem either composed of similar tracheides or with a distinction of central and peripheral xylem.

The Family *Rhyniaceæ* comes into the class of Vascular Cryptogams to which we have given the name of *Psilophytales* (Part I, p. 780), since "the sporangia are borne at the ends of branches of the stem without any relation to leaves or leaf-like organs."

The consideration of more complicated types of the *Psilophytales* can be deferred until *Asteroxylon* is described.

The classification of the plants so far described from the Rhynie peat-bed is therefore as follows:—

PTERIDOPHYTA.

Class. PSILOPHYTALES.

Family. RHYNIACEÆ.

Genera. *Rhynia* (2 species).

*Hornea* (1 species).

COMPARATIVE DISCUSSION.

The Vascular Cryptogams preserved in the Rhynie peat-bed are the most ancient plants of which the internal structure and external morphology are adequately known. They facilitate our understanding of those plants of early Devonian age which are only known as impressions, while these assist in forming a conception of the form and habit of the plants of this remarkable flora. The consideration of this flora as a whole is beyond the scope of the present paper. In this discussion we are concerned only with the simpler types of the Psilophytales which have been placed above in the Family Rhyniaceæ.

The great interest of these plants (*Rhynia*, *Hornea*) is that they acquaint us with a type of construction fundamentally more primitive, not only than that of existing land plants but of most plants composing the Upper Devonian and Carboniferous floras.

Between the Lower and Middle Old Red Sandstone and the Upper Old Red Sandstone or Devonian, as represented by the flora of the Kiltorkan beds, there is a most remarkable difference in the type of plant life. It is doubtful if a single species which occurs in the Lower and Middle Old Red Sandstone of Scotland is present in the Upper Old Red as represented by the Kiltorkan beds. In fact, the botanical affinity of the plants of the latter is with the Lower Carboniferous flora rather than with the Middle and Lower Old Red Sandstone plants.

The type of plant exhibited by *Hornea* and *Rhynia* is the simplest known in undoubted Pteridophyta. We know nothing of the sexual generation, the existence of which there is no reason to doubt, and of the early stages of the sporophyte. The full-grown sporophyte is differentiated into rhizome, stems, and sporangia. It has no leaves or roots. The *rhizome*, which was probably subterranean, was intimately connected to the substratum by long non-septate rhizoids. In *Hornea* it was a tuberous parenchymatous structure from which the stems arose. In *Rhynia* it had a central vascular strand, and is like a peculiar region of the stem. The cylindrical *stems* branched dichotomously, diminishing in diameter. They had a simple vascular system, the stele consisting of a cylindrical strand of xylem surrounded by a zone of phloem. Stomata occurred in the epidermis of *Rhynia*, and there

was a well-developed system of small intercellular spaces. The peculiar hemispherical projections of *Rhynia Gwynne-Vaughani* were the seat of adventitious lateral branches, and, whatever their other functions, may provisionally be regarded as dormant branches. The *sporangia* correspond to transformed and more or less specialised ends of stems of various sizes. Their thick wall was indeliscent, and the epidermis was usually specially thickened. There was a peculiar (and possibly tracheidal) tapetum. The spores were developed in tetrads and had cuticularised walls. No sterile cells were mixed with the spores. In *Hornea* the central tissue formed a sterile columella projecting into the sporangial cavity.

This is a simpler type of plant than is known in any existing Vascular Cryptogam, or in any extinct forms from the Carboniferous period onwards. In the Devonian period, however, there are indications of plants of correspondingly simple morphology. It will be sufficient to mention here *Sporogonites* as possibly related to the Rhyniaceæ.

*Sporogonites exuberans*, Halle,\* from the Lower Devonian rocks of Røragen, Norway, consists of a long unbranched axis terminating in a sporogonial or sporangial structure which is similar to the sporangium of *Hornea* in a number of characters. There are distinct differences, however, but the two agree in the presence of a columella rendering the spore-containing cavity dome-shaped. HALLE regards *Sporogonites* as a sporogonium and as finding its "nearest analogy in the sporogonia of the Bryophyta."† Our fuller knowledge of *Hornea*, however, lends weight to another suggestion of HALLE that "the possibility must be faced that it may represent only the upper part of a more highly developed sporophyte, perhaps on the line of descent of the pteridophytes."‡ So far as the evidence afforded by the remains of *Sporogonites* goes, it does not establish the bryophytic nature of the plant. In showing a general resemblance to sporogonia of Bryophytes the sporangia of *Hornea* and *Rhynia* agree with *Sporogonites*, and in them the relations of the sporangia to the whole simple vascular plant is known.

While the comparisons with *Sporogonites* and with some undescribed impressions which we have seen are of great interest, our fairly complete knowledge of the structure as well as the external morphology of *Rhynia* and *Hornea* makes them more suitable for comparison with other plants. In dealing with such simply organised Pteridophyta comparisons must be widely extended, but at present are best only indicated in outline.

The simple organisation of the sporophytes of *Rhynia* and *Hornea* may therefore be briefly compared with some other Pteridophyta, with Bryophyta, and with Alge.

\* HALLE, T. G., "Lower Devonian Plants from Røragen in Norway," *Kongl. Svensk. Vetenskapsakad. Handlingar*, Bd. 57, 1916, p. 27, pl. iii, figs. 10-32.

† *Loc. cit.*, p. 31.

‡ *Loc. cit.*, p. 40.

## COMPARISONS WITH PTERIDOPHYTA.

In comparing the Rhyniaceæ with other Pteridophyta we are limited by the fact that we are dealing with the simplest types of Vascular Cryptogams known. All the other Vascular Cryptogams, including such archaic forms as *Asteroxylon* and *Psilophyton*, are more highly organised than these rootless and leafless plants, the body of which might as well be termed a cylindrical, branched, vascular thallus as a stem. Thus no detailed comparison with the organisation of the whole plant in the higher Pteridophyta is possible, and what we have to say on this question will find its proper place in dealing with *Asteroxylon*.

We can, however, recognise correspondences with particular structures in some other Pteridophyta, and it is not without interest that some of these affect features which have always appeared aberrant in the plants possessing them. This applies especially to the rootless rhizome, which may be first briefly discussed.

The only rootless Pteridophyta at present known that need be considered are the Psilotaceæ.\* Both *Psilotum* and *Tmesipteris* have rhizomes embedded in the substratum and attached to this by non-septate rhizoids. It is not at present known whether a root is absent from the young sporophyte of *Psilotum* in its development from an embryo, but none is present in plants arising from the minute bulbils† formed on the rhizome. No root is present in the young plant of *Tmesipteris*‡ borne on the prothallus. The resemblance between the rhizomes of *Rhynia* and of the Psilotaceæ is close, and in neither case is there anything suggesting that the rootless condition is other than primitive. Although more complicated in the aerial shoots, the Psilotaceæ appear to have retained the simplicity of the subterranean region characteristic of the most primitive Vascular Cryptogams.

The rhizome of *Hornea*, on the other hand, appears to correspond most closely to that remarkable and much discussed region of the young plants of certain species of *Lycopodium* and of *Phylloglossum* known as the protocorm. As is well known since the investigations of TREUB,§ the young plant of *Lycopodium cernuum* does not at once initiate a shoot and root, but enlarges outside the prothallus (to which it is attached by a small foot) to form a tuberous parenchymatous body. This protocorm is attached to the soil by numerous rhizoids, and bears on its upper side a number of leaves in no apparent relation to a stem-apex; these leaves are termed protophylls. Later a stem bearing spirally arranged leaves develops, and the first root forms at the base of this shoot. The corresponding stage in *L. laterale* and *L. ramulosum*, two New

\* *Salvinia* and some of the smallest Hymenophyllaceæ may be mentioned, but the rootless condition in them appears to be due to reduction.

† SOLMS, *Annales du Jardin Bot. Buitenzorg*, vol. iv, 1884, pp. 139-190.

‡ HOLLOWAY, *Trans. New Zealand Institute*, vol. 1, 1917, pp. 1-44.

§ TREUB, *Annales du Jardin Bot. Buitenzorg*, vols. iv and viii.

Zealand species, the life-history of which has been described by HOLLOWAY,\* attains a much larger size before a stem-apex is differentiated. "This protocormous rhizome plays a much larger and more important part than does the simple protocorm of *L. cernuum*. It constitutes the plant body for a whole season and may even branch. It appears also that in both *L. laterale* and *L. ramulosum* it is able to reproduce itself vegetatively." † The vascular bundles of the more or less numerous protophylls borne on the protocorms of these three species of *Lycopodium* end blindly below in the parenchymatous tissue, the protocorm itself having no vascular system.

The protocorm of *Phylloglossum*, which in the embryo plant resembles that of *L. cernuum*, appears to be repeated as the specialised resting tuber by means of which this plant perennates. This region in *Phylloglossum* can be regarded as both primitive and specialised.

The rootless plant of *Hornea* appears to retain in the adult condition an organisation comparable to the protocorm stage in the species of *Lycopodium* mentioned above. The relation of the aerial stems of *Hornea* to the rhizome is similar to that of the protophylls to the protocorm in *Lycopodium*.

The resemblance of the protocormous rhizome of the ancient Vascular Cryptogam *Hornea* to the protocorm present as a transient embryonic phase in some existing species of *Lycopodium* supports the suggestion made by TREUB as to the nature of the protocorm. He was led to assume "que chez les ancêtres des cryptogames vasculaires actuels un organe a pris naissance qui a dû avoir beaucoup de ressemblance avec le tubercule embryonnaire des Lycopodes." His discussion is summed up thus:—

"Le tubercule embryonnaire chez les Lycopodes est un organe rudimentaire."

"L'organe admis théoriquement chez les ancêtres des Cryptogames vasculaires actuels, et désigné ci-dessus comme 'predecesseur de la pousse feuillée telle qu'elle se présente maintenant chez les plantes vasculaires' existe encore aujourd'hui à l'état passager, dans le genre *Lycopodium*. Cet organe n'est autre que le tubercule embryonnaire."

"Aussi je propose de donner au tubercule embryonnaire des Lycopodes le nom de *protocorme*." ‡

In view of the morphology of *Hornea* it may be said that the existence of this organ does not require to be theoretically assumed in archaic Vascular Cryptogams, but is demonstrated.

So far as the anatomical construction of the Rhyniaceæ is concerned, we can only recognise its simplicity and its direct relation to the primary vegetative functions of land plants, absorption, conduction, aeration, and protection. It is only necessary

\* HOLLOWAY, *Trans. New Zealand Institute*, vol. xlviii, 1915, pp. 253-303.

† *Ibid.*, vol. xlix, 1916, p. 90.

‡ TREUB, *Annales du Jardin Bot. Buitenzorg*, vol. viii, 1890, p. 30.

to recall the rhizoids, the simple vascular strand, the intercellular spaces and stomata, and the thick cuticle to indicate how these needs are met.

The simplicity of the stelar anatomy limits comparison with other vascular plants, but may be compared with the rhizome of the Psilotaceæ. In the xylem of the central cylinder of the Rhyniaceæ we find two grades of construction illustrated: (a) the strand of equivalent and similar tracheides in many stems of *Rhynia Gwynne-Vaughani*; (b) a differentiation of the strand of xylem into smaller inner tracheides and larger peripheral tracheides, as in some stems of *Rhynia Gwynne-Vaughani* and regularly in *R. major* and in *Hornea*. This differentiation suggests comparison with the xylem of the stem-stele and leaf-traces of a number of Pteridophyta in which the protoxylem is surrounded by metaxylem (centrarch).

The sporangia of *Rhynia* and *Hornea* will be compared below with the sporogonia of Bryophyta and the stichidia of the Red Sea-weeds. What in other Pteridophyta may correspond to their simple terminal position will be better discussed in a later paper when the more complicated types of Psilophytales have been considered. A peculiarity of the sporangia of *Rhynia* and *Hornea* is that they are relatively large and indehiscent. The thickened epidermis seems an advance in specialisation, though apparently useless for dehiscence. It looks as if the thickened epidermis, serving for the protection of the spores, had preceded any arrangement for the opening of the sporangium in these plants. The sterile columella of the sporangium of *Hornea* may correspond to the sterile projection from the base of the sporangium in some species of *Lycopodium*.

#### COMPARISONS WITH BRYOPHYTA.

The difficulty in comparing Rhyniaceæ with Bryophyta lies in our ignorance of the sexual generation and the relations of the young sporophyte to it in the ancient Pteridophyta. The simple morphology of the vegetative region of the plants of *Rhynia* and *Hornea* as well as their sporangial structure appear, however, to bring us a step nearer to a comparative morphology of the sporophyte of Vascular Cryptogams and the bryophytic sporogonium. It is sufficient at present to indicate the general resemblances that can be traced between the fertile regions of these Old Red Sandstone plants and the sporogonia of Hepaticæ, of *Anthoceros*, and of certain Mosses. Whether the sporogonium is a simpler parallel development to the sporophyte or is a reduced equivalent of such a plant as that of the Rhyniaceæ must remain an open question. The possibility that these questions, which have hitherto had to be treated in a purely speculative fashion, may be at least partially answered by the discovery of further plants of early Devonian age, is strengthened by the experience of the last few years.

## COMPARISONS WITH ALGÆ.

Without implying direct derivation of the Pteridophytes from any more complex Algæ or actual relationship with any known Algæ, it is impossible to overlook the resemblance in habit between the plant of *Rhynia* and *Hornea* and some Algæ. The comparison is closest with some Red Algæ, which show a distinction of a rhizome-like basal region and cylindrical dichotomously branched axes and have their tetraspores developed within the more or less altered ends of some of the branches. As examples, *Furcellaria fastigiata* and *Cordylecladia (Gracilaria) erecta* may be mentioned. Such resemblances, though they may be superficial, indicate the need of caution in deciding whether impressions of early Devonian plants of this habit were Pteridophyta or Algæ. Formerly a number of these plants, which we now know to be Vascular Cryptogams, were classed as Algæ or Fucoids. We anticipate that others will prove really to be Algæ, and that the comparison between them and the Pteridophyta of the same early geological age will be of peculiar interest.

A more special question concerns the equivalent of the sporangium of the Rhyniaceæ in the Algæ. The tetrads of spores in certain Algæ and the tetrads in the land plants appear to correspond strictly. In some Red Algæ we find the spore-mother-cells (or tetrasporangia) confined to certain special branches, or to the tips of ordinary branches and there situated below the surface. Such special tetraspore-bearing branches are known as stichidia. It is one possible view of the sporangia of Pteridophyta to regard them as the equivalents of such stichidia. The general resemblance and the correspondence in regional anatomy which can be traced between the sporangium of *Hornea* and the less differentiated sporangia of *Rhynia*, on the one hand, and the tetraspore-containing branches of such Algæ as *Cordylecladia*, *Furcellaria*, *Gigartina*, and some Rhodomelaceæ on the other, supports this way of regarding the sporangia of these early Pteridophyta.

We are here probably dealing with a homoplastic similarity which is an expression of general morphology rather than of relationship. The whole question is too wide to be appropriately treated in this place, but the preceding remarks will suffice to indicate the bearing of the new facts upon it. In our ignorance of the complete life-histories and the forms of the sexual and asexual generations, both of the ancient Algæ and of the simplest Pteridophytes, any suggestion of relationship would be dangerous and is not implied in the above comparisons. The facts are, however, consistent with the Rhyniaceæ finding their place near the beginning of a current of change from an Alga-like type of plant to the type of the simpler Vascular Cryptogams.

## CONCLUSION.

If we review the comparisons we have been led to make, it will be evident that all the features of *Rhynia* and *Hornea* point to the Rhyniaceæ illustrating an early

stage in the organisation of the sporophyte of Vascular Cryptogams. On grounds of their general structure it may be presumed that these simple plants were land plants. They are somewhat advanced along the line of progression of the land-growing sporophyte, but not so far as to obliterate clues to the origin of this.

Speculations as to the origin of the sporophyte of the Pteridophyta when broadly considered fall into two groups. On the one hand, it has been suggested that the vegetative organs of the sporophyte have arisen as the result of a process of progressive sterilisation within an interpolated phase of the life-history; this phase in its simplest form was composed wholly of reproductive spores. On the other hand, the origin of the sporophyte of the Pteridophyta has been looked for in the modification of a plant body such as we see in the asexual stage of a number of Algæ; this would have a more or less differentiated vegetative portion bearing asexual reproductive organs.

It appears to us that, while not inconsistent with the first of these two hypotheses, the morphology of the Rhyniaceæ is much more in line with the second. The organisation of *Hornea* and *Rhynia* make the transition assumed by this second hypothesis readily conceivable.

We do not, however, desire to enter at present into a discussion of the general problem or to draw conclusions that would be premature. The interest of *Rhynia* and *Hornea* lies in their providing new and definite historical data on early steps in the evolution of land plants. Since we may hopefully expect further discoveries to make the story more complete, any hypothetical construction of the course of evolution would be superfluous. It is sufficient, without entering into particular theories, to have indicated the bearing of the new facts on some of the chief hypotheses as to the early steps in the origin of land plants that have been entertained by morphologists. That these archaic and simple Pteridophyta should compel us to institute comparisons, not only with some existing Vascular Cryptogams but with bryophytic sporogonia and the organisation of the plant in some Algæ, appears to us pregnant with morphological interest whatever the actual lines of descent may have been.

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#### EXPLANATION OF PLATES.

(All the figures are from untouched photographs.)

#### PLATE I.

*Rhynia Gwynne-Vaughani*, Kidston and Lang.

Fig. 1. A small rhizome (*r.*) in transverse section attached by rhizoids (*rh.*) and giving off laterally an ascending stem (*br.*).  $\times 14$ . (Slide No. 2423.)

Fig. 2. Longitudinal (*a*) and transverse (*b*) sections of apical regions of stems.  $\times 14$ . (Slide No. 2425.)

Fig. 3. The longitudinal section of the apex of a stem shown in fig. 2 (*a*), more highly magnified.  $\times 105$ . (Slide No. 2425.)

- Fig. 4. The transverse section of a stem apex in fig. 2 (*b*).  $\times 105$ . (Slide No. 2425.)
- Fig. 5. Longitudinal section of stem showing incompletely developed tissue with cell contents.  $\times 33$ . (Slide No. 2426.)
- Fig. 6. Basal region of the sporangium shown in Part I, Pl. IX, figs. 63 and 63 (*a*). *ep.*, epidermis; *m.l.*, decayed middle layers of wall; *tap.*, tapetum.  $\times 60$ . (Slide No. 2392.)
- Fig. 7. Apical region of the same sporangium. *ep.*, epidermis; *tap.*, tapetum.  $\times 60$ . (Slide No. 2392.)
- Fig. 8. Sporangium in transverse section. *ep.*, epidermis; *m.l.*, decayed middle layers of wall; *tap.*, tapetum.  $\times 14$ . (Slide No. 2427.)
- Fig. 9. Sporangium in obliquely transverse section full of spores.  $\times 14$ . (Slide No. 2424.)
- Fig. 10. Obliquely longitudinal section of sporangium without tapetum and without specially thickened epidermal layer, the cavity partially filled with fully developed spores.  $\times 14$ . (Slide No. 2423.)
- Fig. 11. Small sporangium in which the mass of spores is enclosed by a wall like the ordinary tissues of the stem.  $\times 33$ . (Slide No. 2428.)
- Fig. 12. Spores in tetrads from the sporangium in fig. 11.  $\times 105$ . (Slide No. 2428.)
- Fig. 13. Mature spores from the sporangium shown in fig. 9.  $\times 160$ . (Slide No. 2424.)

## PLATE II.

*Rhynia major*, Kidston and Lang.

- Fig. 14. Transverse section of a moderately large and well-preserved stem. *ep.*, epidermis; *o.c.*, outer cortex; *i.c.*, inner cortex; *ph.*, phloem; *x.*, xylem; *a*, interruption in outer cortex in relation to a stoma.  $\times 20$ . (Slide No. 2429.)
- Fig. 15. Transverse section of one of the smallest stems met with, showing the relatively large stele.  $\times 20$ . (Slide No. 2430.)
- Fig. 16. Transverse section of stele, photographed to show the phloem.  $\times 33$ . (Slide No. 2431.)
- Fig. 16A. Central portion of specimen seen in fig. 16, photographed with different screen to show details of the xylem. *x.o.*, outer xylem; *x.i.*, central xylem.  $\times 60$ . (Slide No. 2431.)
- Fig. 17. Longitudinal section of stem with well-preserved stele. *o.c.*, outer cortex; *i.c.*, inner cortex; *ph.*, phloem; *x.*, xylem.  $\times 20$ . (Slide No. 2429.)
- Fig. 18. Longitudinal section of stem, the inner cortex and phloem decayed. *o.c.*, outer cortex interrupted at *a* beneath a stoma; *x.*, xylem.  $\times 14$ . (Slide No. 2395.)
- Fig. 19. Transverse section of large stem showing the breaking down of the inner cortex as the result of decay. *o.c.*, outer cortex; *i.c.*, inner cortex; *ph.*, phloem; *x.*, xylem.  $\times 20$ . (Slide No. 2398.)

## PLATE III.

*Rhynia major*, Kidston and Lang.

- Fig. 20. Longitudinal section of stele with the soft tissues preserved. *i.c.*, inner cortex; *ph.* phloem; *x.*, xylem.  $\times 60$ . (Slide No. 2429.)
- Fig. 21. Group of stems compressed in the peat, the one at *a* showing two steles in preparation for dichotomous branching.  $\times 14$ . (Slide No. 2432.)
- Fig. 22. Stele from a stem photographed to show the xylem. *i.c.*, inner cortex; *ph.*, phloem; *x.o.*, outer xylem; *x.i.*, central xylem.  $\times 60$ . (Slide No. 2432.)
- Fig. 23. Transverse section of a large decayed sporangium filled with spores. Only the thickened epidermis is preserved, and this is broken and overlapped at *a*.  $\times 14$ . (Slide No. 2433.)
- Fig. 24. Transverse section of sporangium with well-preserved wall. *ep.*, thickened epidermis; *m.l.*, middle layers of wall; *tap.*, tapetum; *sp.* spores.  $\times 14$ . (Slide No. 2434.)
- Fig. 25. Portion of the silicified peat composed of decayed stems of *Rhynia major* with two sporangia of this species.  $\times 7$ . (Slide No. 2435.)
- Fig. 26. Spores from sporangium in fig. 23.  $\times 160$ . (Slide No. 2433.)

## PLATE IV.

*Hornea Lignieri*, Kidston and Lang.

Fig. 27. Large protocormous rhizome in vertical section with three lobes, a stem arising from each lobe.  $\times 14$ . (Slide No. 2436.)

Fig. 28. Portion of the silicified peat, the matrix of which is composed of decayed stems of *Hornea* with spores scattered throughout. Portions of three rhizomes are shown. The largest is cut vertically and shows two tuberous lobes from each of which a stem arises. A stele is present in each stem.  $\times 14$ . (Slide No. 2437.)

## PLATE V.

*Hornea Lignieri*, Kidston and Lang.

Fig. 29. Vertical section through a rhizome missing the attachment of any stem, but showing the general parenchymatous structure and the distribution of the rhizoids. *o.e.*, outer zone; *i.c.*, inner tissue; *b.t.*, brown-walled tissue in the neighbourhood of the base of a stele.  $\times 14$ . (Slide No. 2438.)

Fig. 30. Portion of the lower surface of a rhizome in vertical section showing the rhizoids springing as protrusions of all the epidermal cells.  $\times 33$ . (Slide No. 2442.)

Fig. 31. Section of portion of the largest rhizome met with. This is a horizontal section of a rhizome below the bases of the steles of a number of stems which arose from it. The brown parenchymatous tissue in relation to some of these is seen at the points marked *b.t.* Lying beside the rhizome at *st.* is an obliquely transverse section of a stem.  $\times 7\frac{1}{2}$ . (Slide No. 2441.)

Fig. 32. Tangential section showing the rhizoid-bearing surface of a rhizome. The bases of the rhizoids are cut across at  $\alpha$ , where they spring from the central portion of each epidermal cell.  $\times 60$ . (Slide No. 2443.)

Fig. 33. The tangential section of the rhizoid-bearing surface from which fig. 32 was taken, showing the long rhizoids extending into the peat.  $\times 14$ . (Slide No. 2443.)

Fig. 34. Small protocormous rhizome (*r.*) with rhizoids (*rh.*) springing as an adventitious growth of the superficial tissues of the main rhizome (*r.*).  $\times 33$ . (Slide No. 2441.)

## PLATE VI.

*Hornea Lignieri*, Kidston and Lang.

Fig. 35. Accurately vertical section of a lobe of a rhizome showing the attachment of a stem. The stele of this on being followed down into the rhizome shows the characteristic base in longitudinal section. The peat around contains spores and decayed stems of *Hornea*.  $\times 14$ . (Slide No. 2444.)

Fig. 36. Base of the stele shown in fig. 35. *x.*, xylem composed of elongated tracheides; *x'*, region with short tracheides passing into an inverted bowl-shaped mass of brown-walled parenchymatous tissue (*b.t.*).  $\times 33$ . (Slide No. 2444.)

Fig. 37. Base of the stem-stele of another specimen showing the same features as fig. 36. *x.*, xylem composed of elongated tracheides; *x'*, region with short tracheides passing into an inverted bowl-shaped mass of brown-walled parenchymatous tissue (*b.t.*).  $\times 33$ . (Slide No. 2445.)

Fig. 38. Vertical section of a rhizome showing good rhizoids and with the characteristic base of a stem-stele displaced downwards through the decay of the inner tissue.  $\times 20$ . (Slide No. 2446.)

Fig. 39. Portion of silicified peat containing fairly well-preserved stems of *Hornea*. These stems, one of which is in longitudinal section, show the structure of the lower region close to the rhizome.  $\times 14$ . (Slide No. 2447.)

## PLATE VII.

*Hornea Lignieri*, Kidston and Lang.

Fig. 40. Slightly oblique transverse section of a small stem, probably from the upper region of the plant. *cut.*, cuticle; *c.*, cortex with indications of outer and inner zones; *ph.*, phloem; *x.*, xylem.  $\times 33$ . (Slide No. 2448.)

Fig. 41. Longitudinal section of stem about 5 mm. above its origin from a rhizome. *ep.*, epidermis; *c.*, cortex with indications of outer and inner zones; *ph.*, phloem; *x.*, xylem.  $\times 33$ . (Slide No. 2440.)

Fig. 42. Transverse section of stem with stele just divided in preparation for dichotomy. *cut.*, cuticle; *c.*, perished cortex; *ph.*, well-preserved phloem; *x.*, xylem.  $\times 33$ . (Slide No. 2446.)

Fig. 43. One of the steles in fig. 42 more highly magnified. *ph.*, phloem; *x.o.*, outer xylem; *x.i.*, central xylem.  $\times 105$ . (Slide No. 2446.)

Fig. 44. Small stem with relatively large stele.  $\times 20$ . (Slide No. 2449.)

Fig. 45. Stele of stem in fig. 44. *x.o.*, outer xylem; *x.i.*, central xylem partially broken down.  $\times 60$ . (Slide No. 2449.)

Fig. 46. Another large stele with broken-down central xylem. *ph.*, phloem; *x.o.*, outer xylem; *x.i.*, position of central xylem.  $\times 33$ . (Slide No. 2450.)

Fig. 47. Transverse section of stem-stele close to the rhizome. *x.o.*, outer xylem; *x.i.*, central xylem.  $\times 60$ . (Slide No. 2447.)

Fig. 48. Transverse section of large stele. *x.o.*, outer xylem; *x.i.*, perished central xylem.  $\times 60$ . (Slide No. 2447.)

Fig. 49. Longitudinal section of xylem of stem-stele showing the continuous outer xylem (*x.o.*) and the central xylem (*x.i.*) interrupted by breaks.  $\times 60$ . (Slide No. 2441.)

## PLATE VIII.

*Hornea Lignieri*, Kidston and Lang.

Fig. 50. Transverse section of stele near its origin from the rhizome. *ph.*, phloem; *x.o.*, outer xylem; *x.i.*, central xylem.  $\times 210$ . (Slide No. 2447.)

Fig. 51. Portion of the stele shown in fig. 47. *ph.*, phloem; *x.o.*, outer xylem; *x.i.*, central xylem.  $\times 210$ . (Slide No. 2447.)

Figs. 52, 53. Tracheides in longitudinal section showing the fine irregularly spiral or reticulate thickening.  $\times 210$ . Fig. 52 (Slide No. 2452); Fig. 53 (Slide No. 2451.)

Fig. 54. Short tracheides from the basal region of a stele showing the fine irregularly spiral or reticulate thickening.  $\times 210$ . (Slide No. 2442.)

Fig. 55. Stele showing dichotomy.  $\times 60$ . (Slide No. 2442.)

Fig. 56. Small stem with stele showing dichotomy.  $\times 20$ . (Slide No. 2452.)

Fig. 57. Small stem *a* showing dichotomously divided stele.  $\times 20$ . (Slide No. 2453.)

## PLATE IX.

*Hornea Lignieri*, Kidston and Lang.

Fig. 58. Portion of peat containing, besides more or less decayed stems of *Hornea*, two slender stems terminating in well-preserved sporangia cut in accurate longitudinal section. The sporangium to the left is bifurcate, that to the right is simple. A portion of the stele (*st.*) is seen in the stalk of each.  $\times 14$ . (Slide No. 2454.)

Fig. 59. Imperfect sporangium in longitudinal section showing flattened top. *w.*, wall; *sp.*, spores; *col.*, columella.  $\times 20$ . (Slide No. 2424.)

Fig. 60. Broad divided sporangium terminating a stalk with two steles (*st.*). *w.*, wall; *sp.*, spores; *col.*, columella.  $\times 20$ . (Slide No. 2456.)

Fig. 61. Portion of peat with spores of *Hornea* distributed through it, and containing on the left a small stem (*a*) and on the right an obliquely-cut sporangium (*b*) showing the characteristic stele of *Hornea*.  $\times 14$ . (Slide No. 2455.)

Fig. 62. Oblique section of the base of a sporangium showing the continuity of the tissue of the columella with the phloem of the stele. *w.*, wall; *sp.*, spores; *col.*, columella; *ph.*, phloem; *x.*, xylem.  $\times 60$ . (Slide No. 2456.)

Fig. 63. Transverse section of a large partially divided sporangium with a single cavity, but the columella

showing two lobes, one of which is again subdividing. *w.*, wall; *tap.*, tapetum; *col. a.*; *col. b.*; *col. b'*, the three divisions of the columella.  $\times 20$ . (Slide No. 2457.)

Fig. 64. Sporangium in transverse section lying beside a longitudinal section of a stem. *w.*, wall; *sp.*, spores; *col.*, columella.  $\times 20$ . (Slide No. 2457.)

## PLATE X.

*Hornea Lignieri*, Kidston and Lang.

Fig. 65. Portion of transverse section of a sporangium of *Hornea*. *ep.*, epidermis; *m.l.*, middle layers of wall; *tap.*, tapetum; *sp.*, spores; *col.*, columella.  $\times 60$ . (Slide No. 2458.)

Fig. 66. Transverse section of a sporangium showing the thickened epidermis. *ep.*, epidermis; *m.l.*, middle layers of wall; *tap.*, tapetum; *col.*, columella.  $\times 20$ . (Slide No. 2456.)

Fig. 67. Portion of wall of sporangium in fig. 66 more highly magnified. *ep.*, epidermis with thickened outer walls; *m.l.*, perished middle layers of wall; *tap.*, tapetum.  $\times 60$ . (Slide No. 2456.)

Fig. 68. Fragment of the epidermis of a broken sporangium showing the thickening of the outer walls extending on to the lateral walls.  $\times 60$ . (Slide No. 2439.)

Fig. 69. Portion of one of the sporangia in fig. 58 showing the columella in longitudinal section. *w.*, wall; *sp.*, spores in the dome-shaped cavity lined by the tapetum (*tap.*).  $\times 60$ . (Slide No. 2454.)

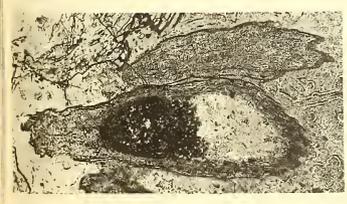
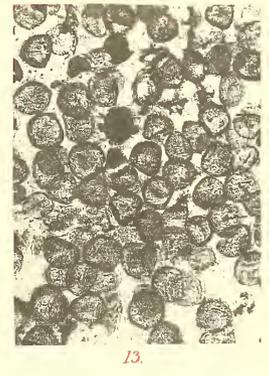
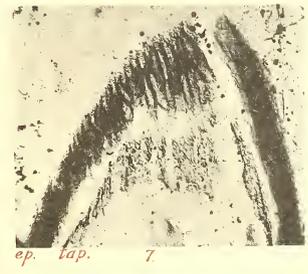
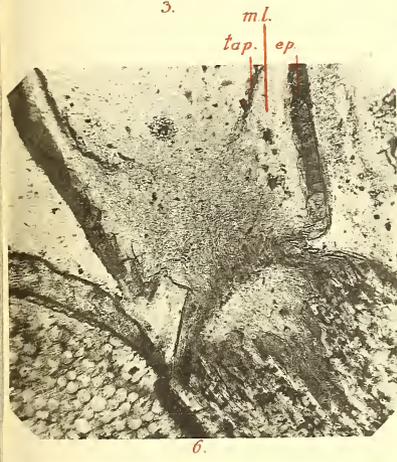
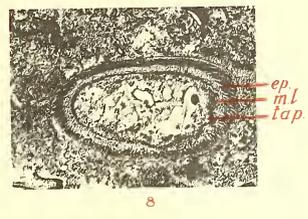
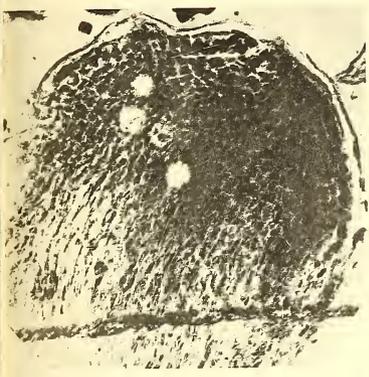
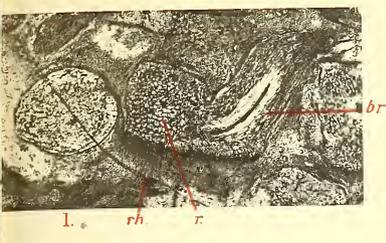
Fig. 70. Portion of a tangential section of a sporangium to show the persistent tapetum. *w.*, wall; *tap.*, tapetum.  $\times 60$ . (Slide 2451.)

Fig. 71. Spores in tetrads around the columella (*col.*).  $\times 105$ . (Slide No. 2459.)

Fig. 72. Mature spores in sporangium. *col.*, columella.  $\times 160$ . (Slide No. 2456.)

We again gratefully acknowledge our indebtedness to the Executive Committee of the Carnegie Trust for a grant to defray the expense of the plates illustrating this memoir.

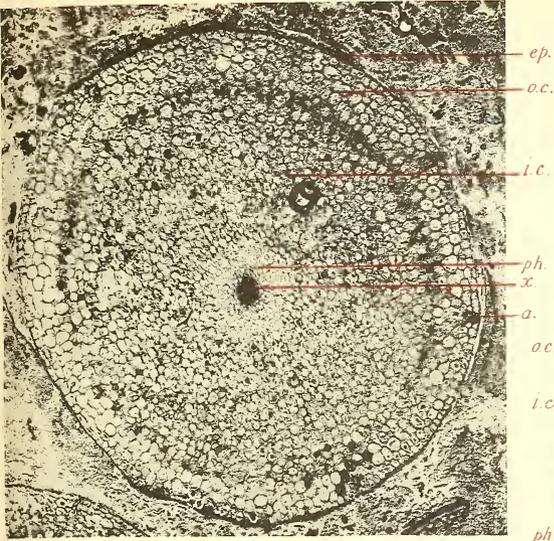




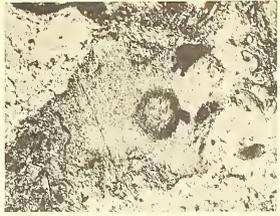
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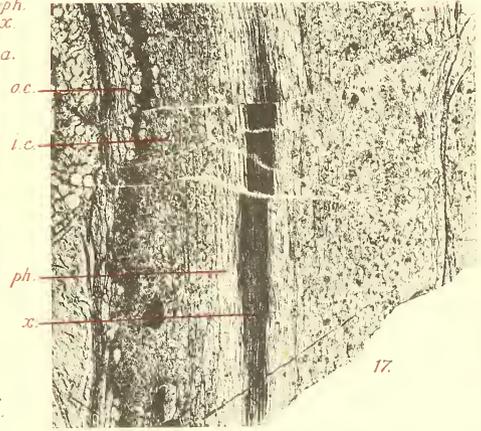




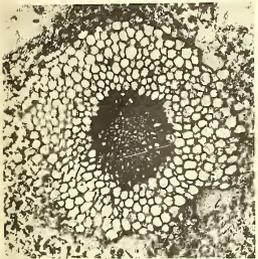
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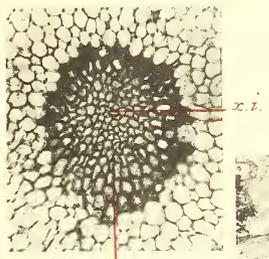
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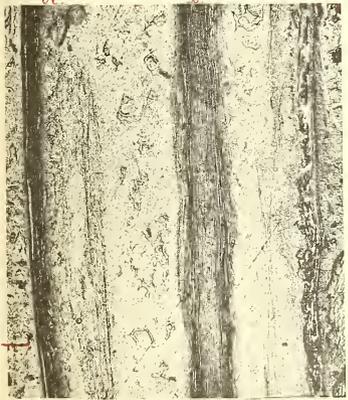
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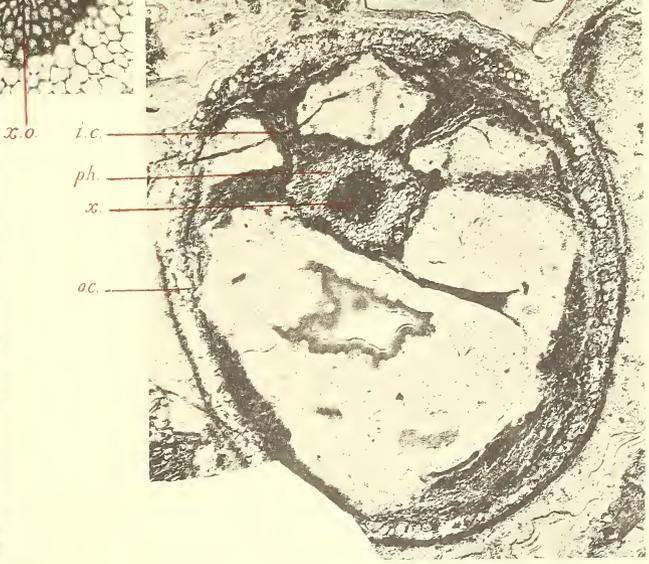
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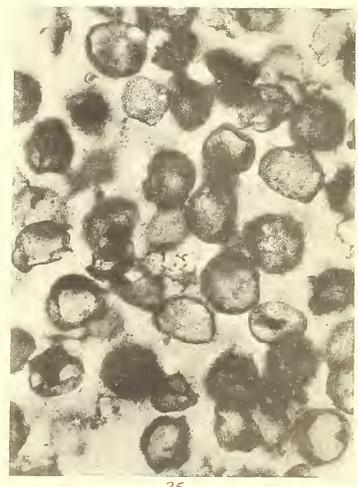
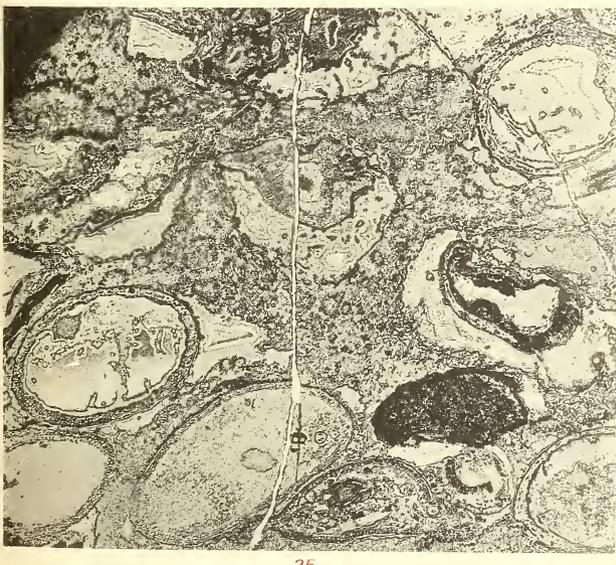
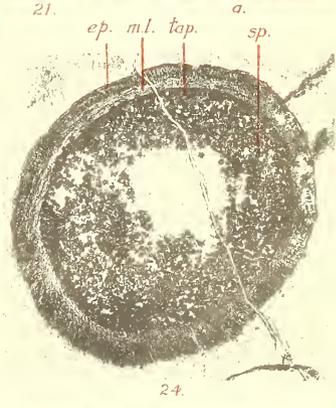
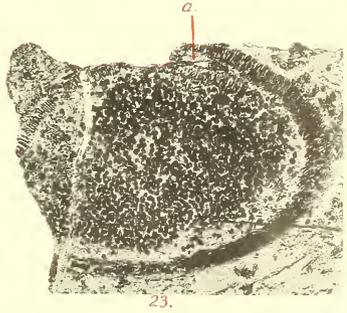
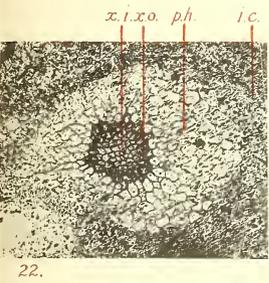
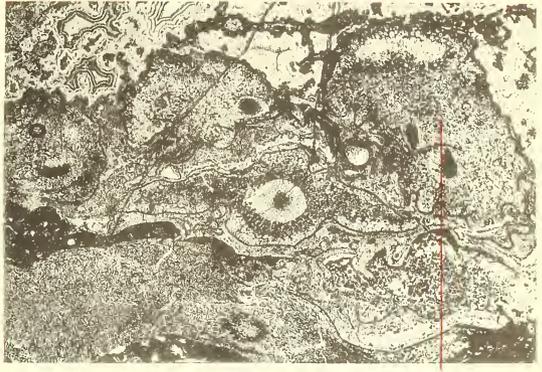
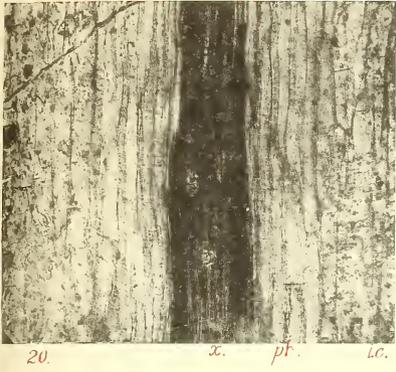
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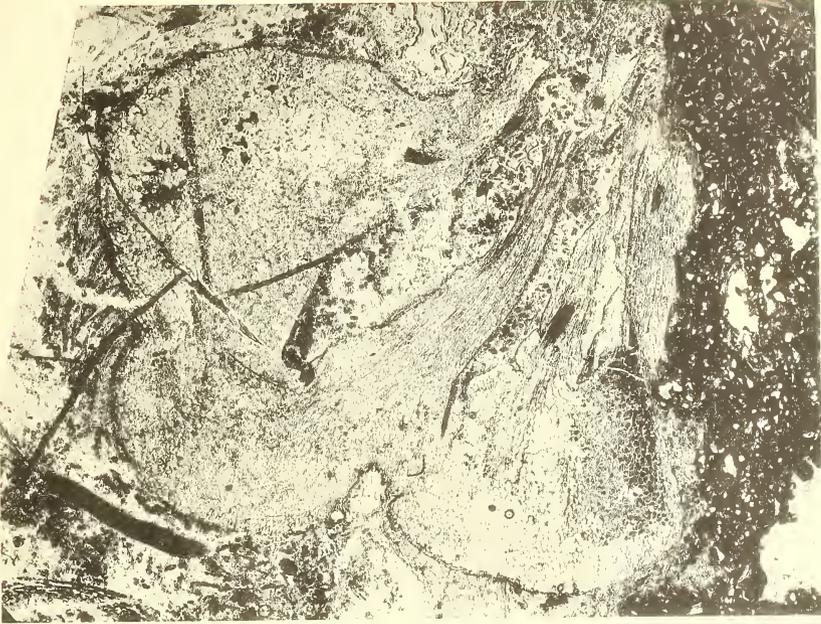
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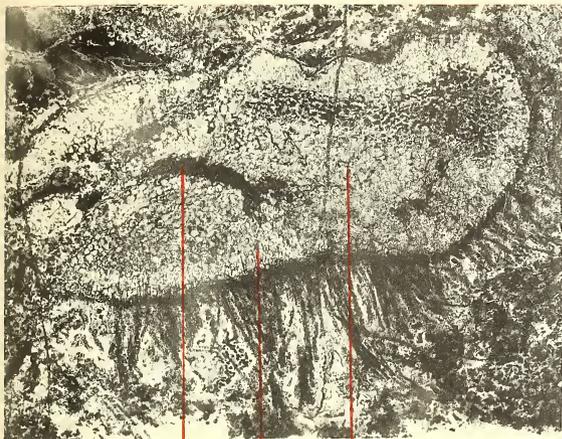
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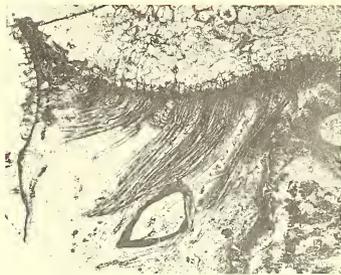
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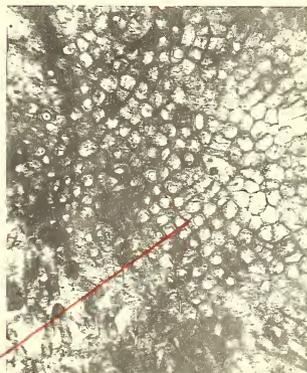




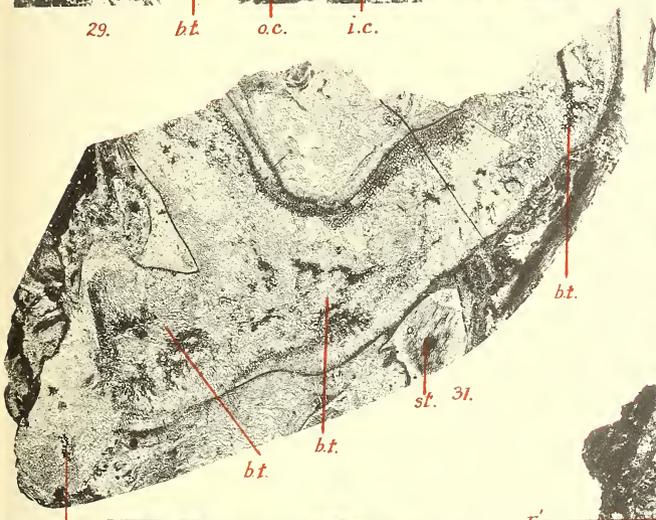
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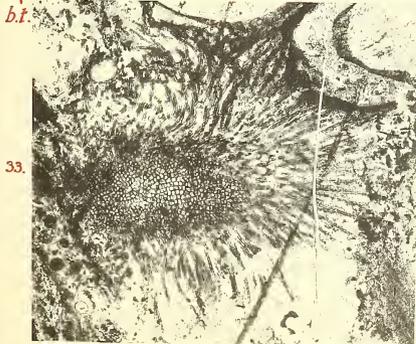
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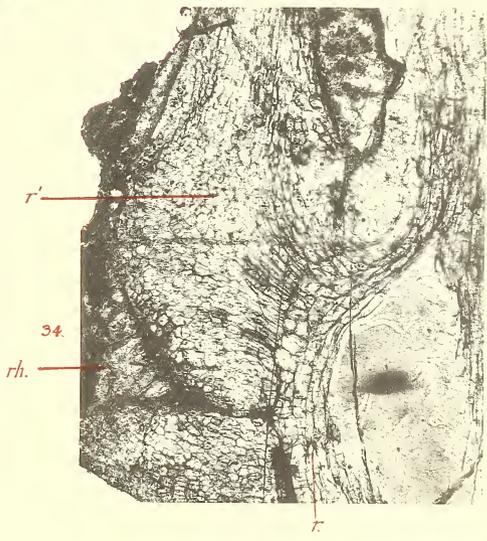
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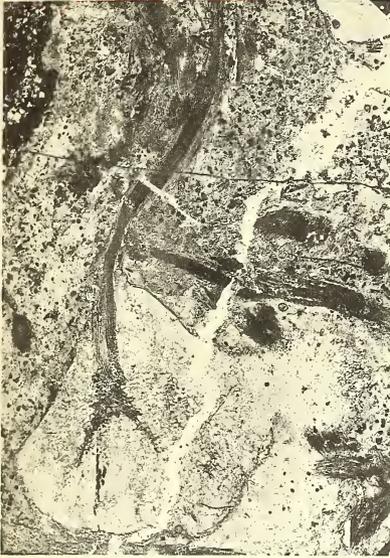


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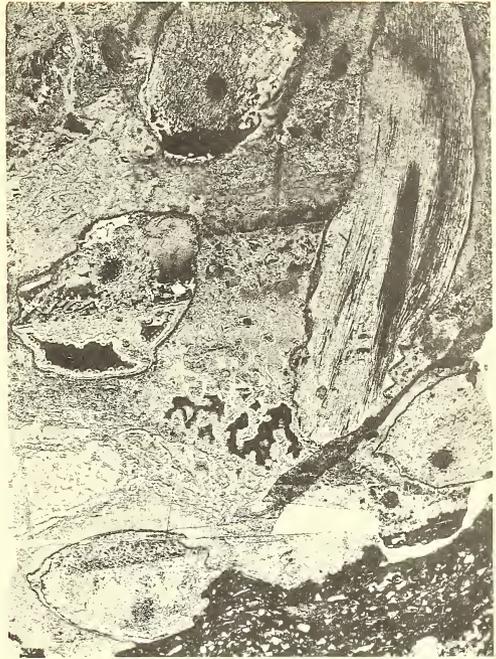


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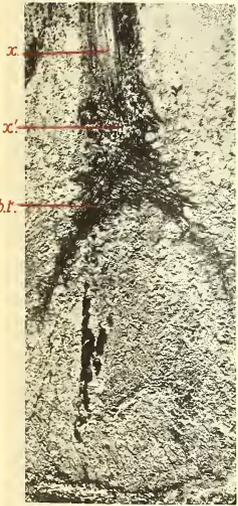




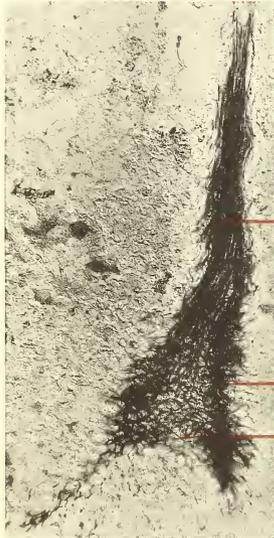
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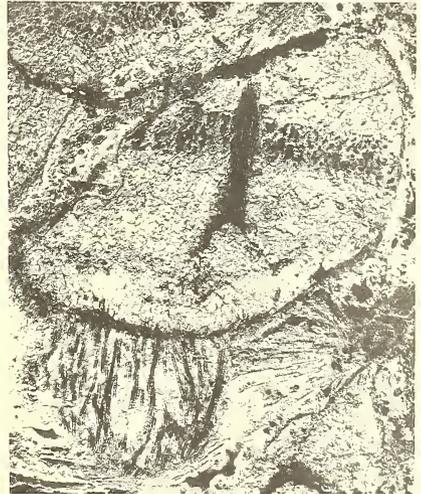
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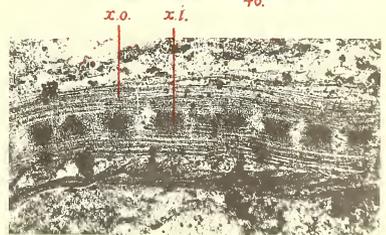
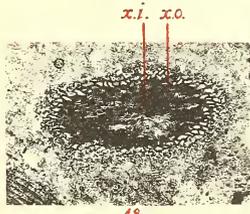
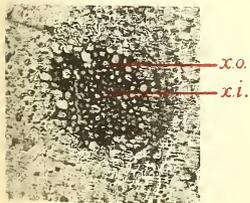
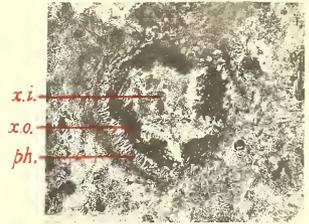
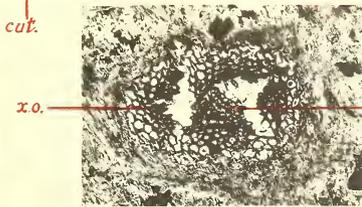
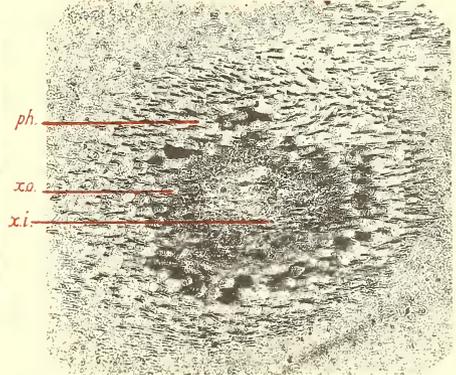
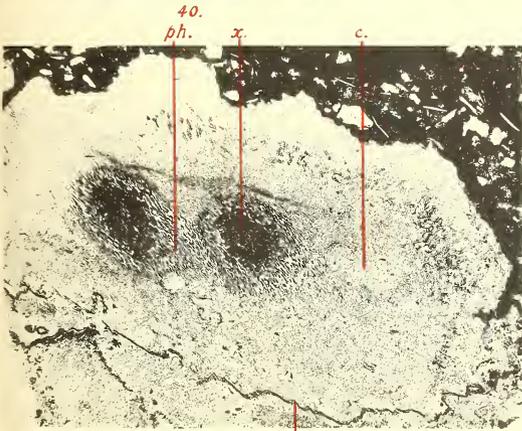
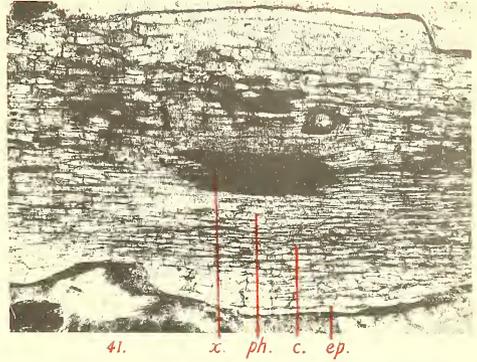
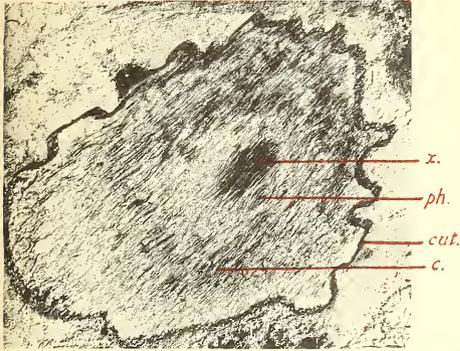
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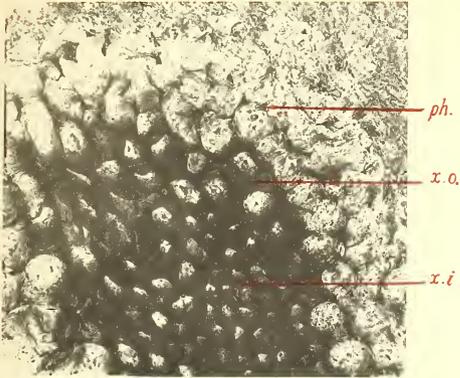




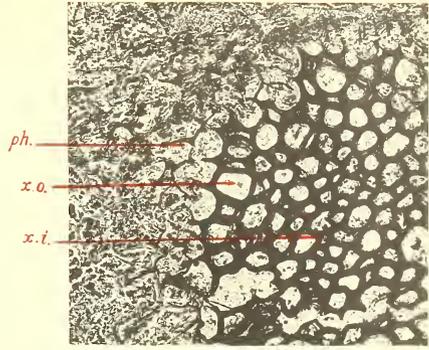
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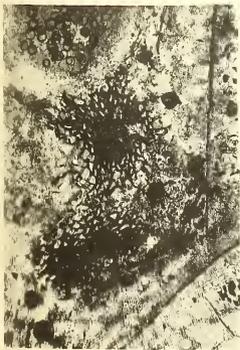
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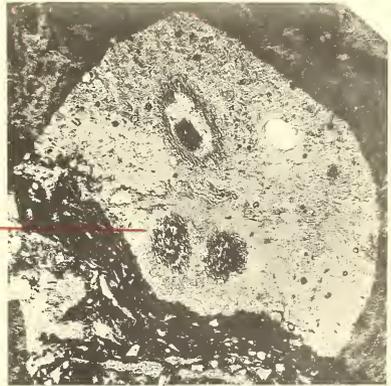
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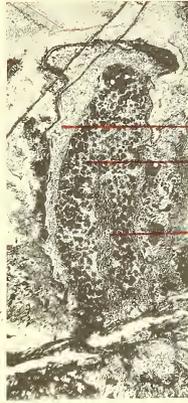
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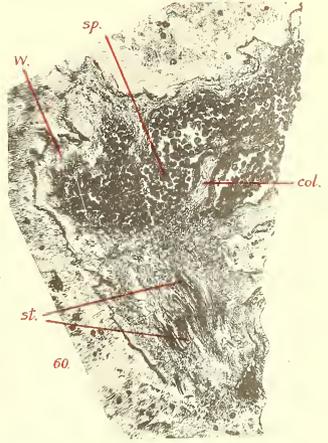




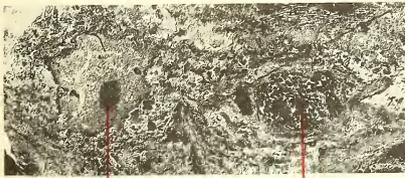
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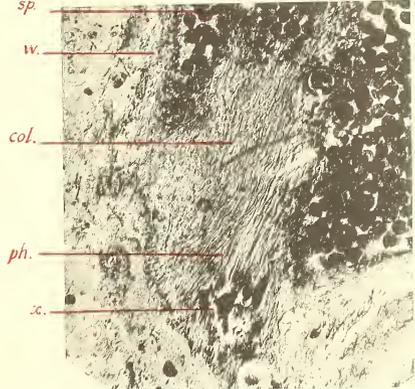
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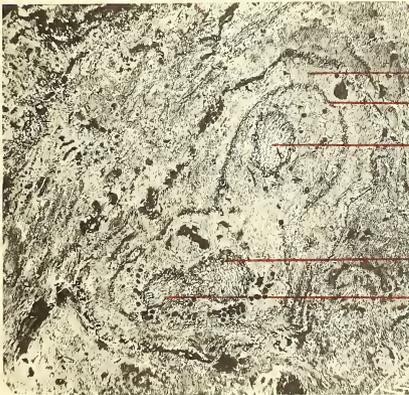
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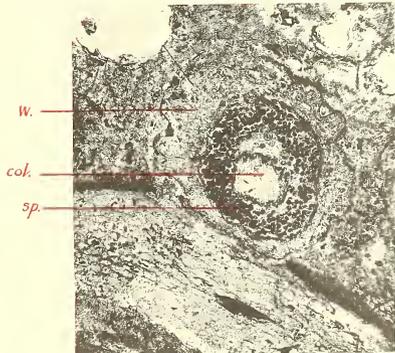
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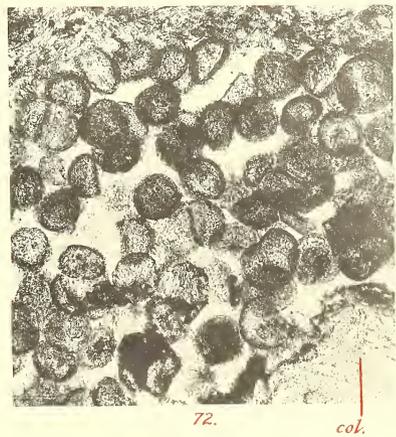
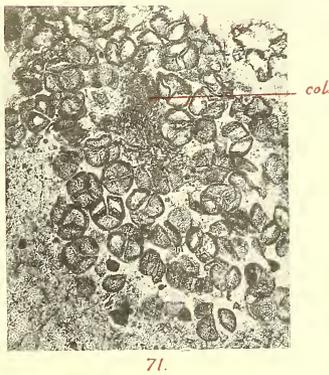
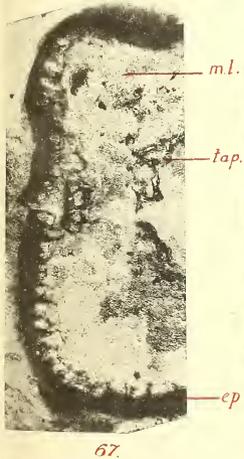
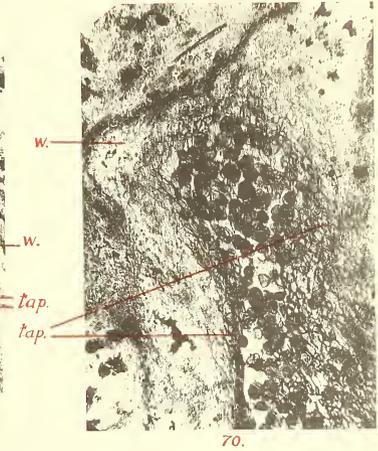
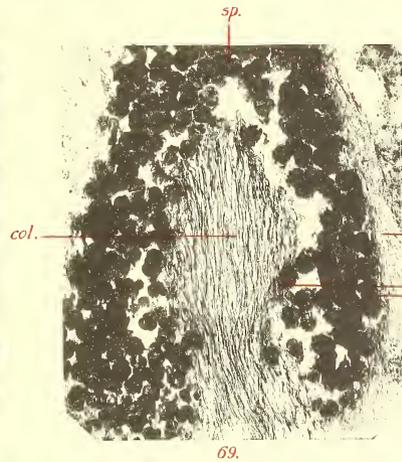
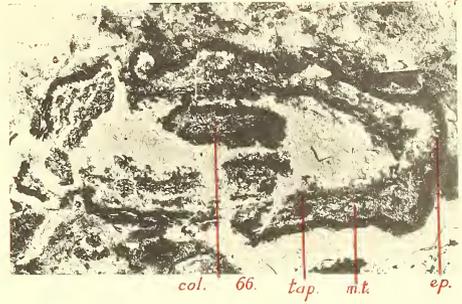
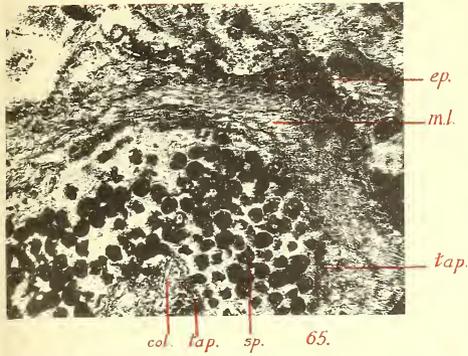


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## XXV.—Theoretical Determination of the Longitudinal Seiches of Lake Geneva.

By A. T. Doodson, R. M. Carey, and R. Baldwin, Tidal Institute, University of Liverpool. *Communicated by* Dr E. M. WEDDERBURN.

(MS. received November 11, 1919. Read January 12, 1920. Issued separately April 2, 1920.)

1. The theoretical determination of the longitudinal seiches of a lake was reduced by Professor CHRYSTAL\* to the finding of those solutions of the differential equation

$$\frac{d^2V}{dx^2} + \frac{\lambda}{p(x)}V = 0 \quad (1)$$

which vanish at  $x = 0$  and  $x = a$ .

Here  $x$  denotes the area of the surface of the lake from one end up to any transverse section, and ranges from 0 to  $a$ ,  $a$  being the total area of the surface of the lake;  $p(x)$  denotes the product of the area of the transverse section at  $x$  and its breadth at the free surface;  $\lambda = \sigma^2/g$ ,  $\sigma$  being the "speed" of the periodic motion and  $g$  the acceleration due to gravity;  $V$  denotes the total volume of water which has passed the section up to the time  $t$ .

If  $\zeta$  denotes the elevation of the free surface at the transverse section corresponding to  $x$ , we have

$$\zeta = -\frac{\partial V}{\partial x} \quad (2)$$

An inverted graph of the function  $p(x)$  was called by CHRYSTAL the "normal curve" of the lake, and it can be constructed from the results of a bathymetrical survey. By approximating to the normal curve by geometrically simple curves, CHRYSTAL showed how to find the required solutions of (1), and he and E. M. WEDDERBURN applied the method to Lochs Earn and Treig.† The normal curves of these lakes are fairly regular, and results were obtained closely in agreement with observation.

In a recent paper by J. PROUDMAN,‡ a general solution of the problem has been given which does not involve approximations similar to those of CHRYSTAL, and the object of the present paper is to give details and results of the application of this solution to Lake Geneva. The normal curve of Lake Geneva had been constructed some years ago by WEDDERBURN; he suggested that the present method should first be applied to this lake, and very kindly supplied his data and calculations. A glance at the diagrams illustrating the normal curve will show how complex the curve is; the approximate methods introduced by CHRYSTAL were not easily or satisfactorily

\* "Hydrodynamical Theory of Seiches," *Trans. Roy. Soc. Edin.*, vol. xli, p. 599.

† "Calculation of the Periods and Nodes of Lochs Earn and Treig," *ibid.*, p. 823.

‡ "Free and Forced Longitudinal Tidal Motion in a Lake," *Proc. Lond. Math. Soc.*, series 2, vol. xiv, p. 240.

applied. A noteworthy feature of PROUDMAN'S method is that it can take account of all the natural irregularities of the body of water, and its application has been found to give very satisfactory results. In §§ 9-11 will be found a comparison between observations and the results of the theoretical determination of the longitudinal seiches of Geneva; better agreement could hardly be expected.

GENERAL ACCOUNT OF THE METHOD.

2. *Mathematical Basis.*

The solution we are using involves the function

$$R(\xi, \eta, \lambda) \equiv \sum_{n=0}^{\infty} (-\lambda)^n I_n(\xi, \eta) \quad . \quad . \quad . \quad (3)$$

where

$$I_0(\xi, \eta) = \eta - \xi \quad . \quad . \quad . \quad (4)$$

and

$$I_n(\xi, \eta) = \int_{s=\xi}^{\eta} \int_{z=\xi}^{s'} \frac{I_{n-1}(\xi, s)}{p(s)} ds ds' \quad . \quad . \quad . \quad (5)$$

$$= \int_{s=\xi}^{\eta} \int_{s=s}^{\eta} \frac{I_{n-1}(s, \eta)}{p(s)} ds ds' \quad . \quad . \quad . \quad (6)$$

for  $n > 0$ .

The functions  $I_n(\xi, \eta)$  depend only on the transverse sections corresponding to  $x = \xi, x = \eta$ , and the variable  $x$  may be measured from either end of the lake, provided that  $\xi$  always refers to that section which is the nearer to that end; that is,  $\xi$  is less than  $\eta$ . This is obviously true for  $n = 0$ , and its general truth can then be readily seen from (5) and (6).

The conditions of the problem are such that the solution is given by

$$R(0, a, \lambda) = 0 \quad . \quad . \quad . \quad (7)$$

A value of  $\lambda$  which satisfies the above equation will then determine the period of a free oscillation; if possible values of  $\lambda$  are denoted by  $\lambda_1, \lambda_2, \dots, \lambda_s, \dots$ , then the periods are given by

$$T = 2\pi / (g\lambda_s)^{\frac{1}{2}} \quad . \quad . \quad . \quad (8)$$

and the corresponding mode of motion is given by

$$V = R(0, x, \lambda_s) \quad . \quad . \quad . \quad (9)$$

on omitting a factor which is a simple harmonic function of the time. We shall then have

$$\zeta = - \sum_{n=0}^{\infty} (-\lambda_s)^n V'_n(0, x) \quad . \quad . \quad . \quad (10)$$

where

$$V'_n(0, x) = \frac{d}{dx} I_n(0, x).$$

Thus the problem resolves itself into finding the functions  $I_n(0, x)$ ,  $I'_n(0, x)$ , which are determined from (5) as

$$I'_n(0, x) = \int_0^x \frac{I_{n-1}(0, s)}{\nu(s)} ds \quad (11)$$

$$I_n(0, x) = \int_0^x I'_n(0, s) ds \quad (12)$$

with the initial form

$$I_0(0, x) = x \quad (13)$$

### 3. Arrangements for Computation.

It is clear that if  $\nu(\alpha)$  is zero the integrands in (5) and (6) become infinite for  $s = \alpha$ . These infinities, however, can be avoided in a very elegant manner as follows.

Equation (35) of the paper by J. PROUDMAN, already quoted, gives the relation

$$R(x, \eta, \lambda) \frac{\partial}{\partial x} R(\xi, x, \lambda) - R(\xi, x, \lambda) \frac{\partial}{\partial x} R(x, \eta, \lambda) = R(\xi, \eta, \lambda) \quad (14)$$

which is a direct consequence of the fact that  $R(\xi, x, \lambda)$  and  $R(x, \eta, \lambda)$  are two solutions of the fundamental differential equation. If these functions be expressed as power series in  $\lambda$  by (3), and the coefficients of  $\lambda^n$  equated, we have

$$\sum_{r=0}^n \left\{ I_{n-r}(x, \eta) \frac{\partial}{\partial x} I_r(\xi, x) - I_r(\xi, x) \frac{\partial}{\partial x} I_{n-r}(x, \eta) \right\} = I_n(\xi, \eta) \quad (15)$$

Hence, if the functions  $I_n(0, x)$  and  $I_n(x, \alpha)$  are known, together with their first differential coefficients with respect to  $x$ , the value of  $I_n(0, \alpha)$  can be at once determined, and no infinities occur in any of the integrands.

We have already pointed out that the variable  $x$  may be measured from either end of the lake, but we have assumed that  $\xi$  is less than  $\eta$ . It is now convenient to split the lake into two portions at some arbitrary point  $x = X$ . Let measurements from the west end of the lake yield the functions  $I_n(0, X)$  and  $I'_n(0, X)$ , and let measurements from the east end yield the functions  $I_n(X, \alpha)$ ,  $I'_n(X, \alpha)$ . Wherever necessary, the system will be denoted by  $w$  or  $e$  to indicate the manner of measuring the variable, so that we have

$$I_n^w(\xi, \eta) = I_n^e(a - \eta, a - \xi) \quad (16)$$

and, if  $x' = a - x$ ,

$$I_n^w(x, \eta) = I_n^e(a - \eta, a - x) = I_n^e(a - \eta, x') \quad (17)$$

$$\frac{\partial^w}{\partial x^2} I_n^w(x, \eta) = \frac{\partial^e}{\partial x^2} I_n^e(a - \eta, a - x) = - \frac{\partial^e}{\partial x'^2} I_n^e(a - \eta, x') \quad (18)$$

In particular, our problem requires the functions for which  $\xi = 0$  and  $\eta = \alpha$ . We shall choose  $X$ , the arbitrary value of  $x$ , to be such that the corresponding section divides the lake into two equal surface areas; that is,  $X = \frac{1}{2}\alpha$ . Let dashes denote differentiation with respect to  $x$  or to  $x'$ , according to the system; then we shall

require  $I_n(0, x)$  and  $I'_n(0, x)$  in both systems for values of  $x$  from 0 to  $\frac{1}{2}\alpha$ , and equation (15) yields

$$\sum_{r=0}^n (I_{n-r} I'_r + I'_{n-r} I_r) = I_n(0, \alpha) \quad (19)$$

where, on the left-hand side, the arguments are  $(0, \frac{1}{2}\alpha)$ .

#### 4. Determination of Periods and Elevations.

The unit of length will be chosen so that the surface of the lake has two units of area, and this unit of length will be called a "lake unit." Thus we have  $\alpha = 2$ , and all the functions on the left-hand side of (19) will have the arguments  $(0, 1)$ .

It is therefore necessary to evaluate the functions  $I_n(0, x)$ ,  $I'_n(0, x)$  from  $x = 0$  to  $x = 1$  in both systems, and substitution in (19) will give the values of  $I_n(0, 2)$  for the whole lake. These determine the value of  $\lambda$  for which  $R(0, 2, \lambda)$  is zero, or, by (3), for which

$$\sum_{n=0}^{\infty} (-\lambda)^n I_n(0, 2) = 0 \quad (20)$$

The elevation  $\zeta$  is then obtained as in equation (10); use is made of the values of  $I'_n(0, x)$  in both systems, and the two sets of values are combined as follows. Reference to (14) shows that when  $R(0, 2, \lambda_s)$  is zero we have

$$R(x, 2, \lambda_s) \frac{\partial}{\partial x} R(0, x, \lambda_s) = R(0, x, \lambda_s) \frac{\partial}{\partial x} R(x, 2, \lambda_s) \quad (21)$$

whence

$$R(0, x, \lambda_s) / R(x, 2, \lambda_s) \text{ is independent of } x \quad (22)$$

Consequently

$$\frac{\partial}{\partial x} R(0, x, \lambda_s) / \frac{\partial}{\partial x} R(x, 2, \lambda_s) \text{ is independent of } x \quad (23)$$

and the values of the elevation in the  $w$ -system are a constant multiple of those in the  $e$ -system. The two systems can thus be fitted together at the point  $x = 1$ . The relation (21) also affords a verification of the value of  $\lambda_s$  obtained from (20).

### APPLICATION TO LAKE GENEVA.

#### 5. Construction of Normal Curve.

The chart used by WEDDERBURN was that of HORNLMANN and DELEBECQUE, *Atlas des lacs français*, with a horizontal scale of 1/50,000, and with the depths stated in metres. He had drawn across it thirty-one lines as the surface traces of transverse sections. The lengths of these lines were measured, and the area of the corresponding transverse section calculated. The product of these two quantities gave the corresponding value of  $p(x)$ . The area of the lake from one end up to a transverse section was measured by means of a planimeter, thus giving  $x$ , and the value of a lake unit was found to be  $u = 1.7052 \times 10^6$  centimetres. The original data are given in Table I, and from them were deduced Tables II and III, which give the values of  $p(x)$  at intervals of 0.01 in  $x$ . The normal curve for Geneva is illustrated in fig. 1, and fig. 2 shows on a larger scale the western portion of the

curve. It will be seen that a large number of peaks exist, and it was necessary, therefore, to provide a very smooth curve in order to avoid excessive numerical errors due to the use of integration formulæ. This was obtained by plotting from the original data, and the nominal accuracy of the interpolated values was

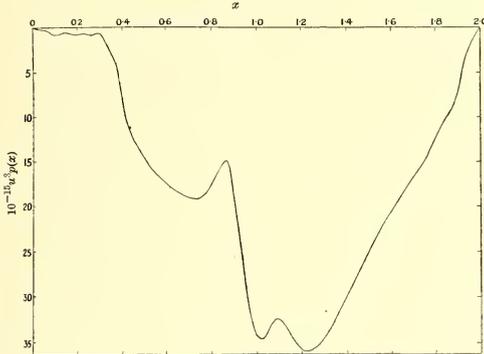


FIG. 1.

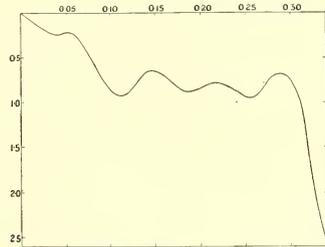


FIG. 2.

increased by redrawing on a greater scale. Great care was taken in smoothing the curve. For the small values of  $x$ , in both systems, the graph of  $x/p(x)$  was used in this smoothing process.

6. *Computation of  $I_n(0, x)$  and  $I'_n(0, x)$ .*

Let  $w(x)$  and  $e(x)$  denote the reciprocal of  $10^{-15}u^3p(x)$  in the  $w$ -system and  $e$ -system respectively; these were calculated at intervals of 0.01 in  $x$ . We now have to apply formulæ (11) and (12). The integration was performed by means of the well-known Simpson formula

$$3 \int_0^{2h} y dx = h[y_0 + 4y_h + y_{2h}] \tag{24}$$

where  $h = 0.01$  in the present instance.

Successive application of this formula gives the values of three times the integral for  $x = 0, 2h, 4h \dots$ , and, by a second series of calculations, for  $x = h, 3h, 5h, \dots$ . The odd and even series are thus calculated independently, and a check on the end values is practically sufficient; this check was performed by means of the interpolation formula

$$16y_{2h} = -y_0 + 9y_{2h} + 9y_{4h} - y_{6h} \tag{25}$$

Thus any term in the odd series can be calculated by interpolation from the even series and compared with the value obtained from the Simpson integration.

In the actual calculations powers of three were retained and powers of ten ignored until all the integrations were completed.

Since  $I_0(0, x) = x$ , the first procedure was to evaluate  $xw(x)$ , and the accuracy of



The extreme columns give the values of  $\kappa^{-n}I_n^w$  and  $\kappa^{-n}I_n^e$ , and are written with the values of  $n$  increasing up the column. The central portion of the table is supposed to be written on a separate piece of paper, so that it can slide up and down between the extreme columns. The values of  $\kappa^{-n}I_n^e$  are written, with  $n$  increasing down the column, on the left-hand side of this central piece and in proximity to  $\kappa^{-n}I_n^w$ ; similarly  $\kappa^{-n}I_n^w$  is written in proximity to  $\kappa^{-n}I_n^e$ . The middle column contains the values of  $\kappa^{-n}I_n(0, 2)$  as calculated from equation (21), and the calculation is easily accomplished. Suppose the value of  $\kappa^{-6}I_6(0, 2)$  be required; then the central piece is moved down until the value  $n=6$  on it is opposite to  $n=0$  on the fixed sheet; the terms of the various products of (19) are then contiguous, and the whole process can be rapidly performed on a calculating machine. The table given shows the arrangement for  $n=6$ , and the central movable piece is enclosed by double lines.

$\kappa^{-n}I_n^w$	$n$	$n$	$\kappa^{-n}I_n^e$	$\kappa^{-n}I_n(0, 2)$	$\kappa^{-n}I_n^w$	$n$	$n$	$\kappa^{-n}I_n^e$
[.00000004]	13						13	
[.00000072]	12						12	
[.00001065]	11						11	
[.00013349]	10						10	
.00140154	9						9	
.012096	8						8	[.000000 00660]
.083874	7						7	[.000000 2578]
.45376	6	0	1.00000	2.0000	1.0000	0	6	.000007 9728
1.8445	5	1	1.84296	18.5144	9.4035	1	5	.000186 982
5.3519	4	2	.82141	55.5745	22.9944	2	4	.003154 1
10.3037	3	3	.163192	84.9787	25.8675	3	3	.035646
11.7405	2	4	.018270	79.3360	16.5171	4	2	.24352
6.4240	1	5	.0013098	50.0488	6.7554	5	1	.84389
1.0000	0	6	.00006522	22.7913	1.9182	6	0	1.00000
		7	[.000002387]	7.8521	.40085		7	
		8	[.000000067]	2.1201	.064320		8	
		9		.46111	.008187		9	
		10		.08258	[.0008485]		10	
		11		.012399	[.00007313]		11	
		12		.0015844	[.00000533]		12	
		13		.00017452	[.00000034]		13	

9. Determination of the Periods.

The solution of the period equation (20) is best effected by the use of HORNER'S method. Let the notation  $J_n = \kappa^{-n}I_n(0, 2)$  be used; then we have to solve the equation

$$J_0 - (\kappa\lambda)J_1 + (\kappa\lambda)^2J_2 - \dots + (-\kappa\lambda)^rJ_r = 0,$$

where  $J_r$  is the last term considered. The accuracy of the solution will be affected

by the omission of the subsequent terms, but the relative importance of the various terms, and the accuracy of the solution, can be tested afterwards. Since the most important terms are those for which  $n$  is small, it is best to deal with the series

$$J_0\mu^n - J_1\mu^{n-1} + J_2\mu^{n-2} - \dots + (-1)^r J_r = 0 \quad (27)$$

where

$$\mu = 1/(\kappa\lambda). \quad (28)$$

The result of HORNER'S method is to give the first three roots as follows:—

$$\left. \begin{aligned} \mu_1 &= 5\cdot2764, & \kappa\lambda_1 &= \cdot18952 \\ \mu_2 &= 1\cdot1725, & \kappa\lambda_2 &= \cdot8529 \\ \mu_3 &= \cdot7459, & \kappa\lambda_3 &= 1\cdot3407 \end{aligned} \right\} \quad (29)$$

We have now to estimate the accuracy of these results. In the first place, the accuracy of the work, regarding  $J_0, J_1, \dots$  as absolutely accurate, may be tested by substituting the above values of  $\kappa\lambda$  on the right-hand side of the equation

$$(\kappa\lambda)J_1 = J_0 + (\kappa\lambda)^2J_2 - (\kappa\lambda)^3J_3 + \dots,$$

whence division by  $J_1$  should give the value of  $\kappa\lambda$ ; the effect of terms beyond  $J_r$  is easily estimated by this process, and it was shown that the values of  $\kappa\lambda$  as given above were not affected, to the order given, by taking terms beyond  $J_{13}$  into account. But the  $J$ 's are only known to a limited degree of accuracy, and this is not great enough for the third decimal of  $\kappa\lambda_2$  to be considered as more than approximately correct, and the second decimal of  $\kappa\lambda_3$  is only an approximation. The value of  $\kappa\lambda_1$ , however, is probably correct to at least four decimals.

The actual periods are given by the relation

$$T = 2\pi/(g\lambda_3)^{\frac{1}{2}}, \quad (30)$$

where  $g$ , expressed in lake units, has the value 980·7 divided by  $1\cdot7052 \times 10^6$ . Introducing the factor  $\kappa$  once for all, we have

$$T = 2\pi\kappa^{\frac{1}{2}}g^{-\frac{1}{2}}\mu_3^{\frac{1}{2}} = 32\cdot41\sqrt{\mu_3} \text{ minutes} \quad (31)$$

Therefore, the values of the first three periods are respectively

$$\left. \begin{aligned} T_1 &= 74\cdot45 \text{ minutes,} \\ T_2 &= 35\cdot1 \text{ ,,} \\ T_3 &= 28 \text{ ,,} \end{aligned} \right\} \quad (32)$$

and all the figures here given may be regarded as significant.

### 10. Determination of the Elevation $\zeta$ and of the Nodes.

The elevation  $\zeta$  may be calculated by the formula

$$\zeta = - \sum_{n=0}^{\infty} (-\kappa\lambda)^n \kappa^{-n} I_n'(0, x),$$

and this function is given in Table VIII at intervals of 0·1 in  $x$ . The value of  $x$  is measured from the western end. Application of the method discussed in § 4 was



was only able to place them approximately. He places the node of the uninodal oscillations somewhere to the west of the line Rolle-Thonon; but he also records that no uninodal oscillation was observed at Séchex or at Fleur D'Eau. Our calculations place the nodal line about 2 km. west of the latter line.

The western node of the binodal oscillations was not observed by FOREL, but he places the eastern node as being approximately on the transversal through Morges; the calculated value for this node gives it as the transversal about 2 km. east of the transversal through Morges.

When it is considered that the exact determination of nodes by observation is very difficult, and when allowance is made for differences in mean lake level, the results that have been obtained by calculation may be regarded as extremely good, and they indicate that the method gives a most satisfactory solution of the problem of free longitudinal motion in a lake.

#### 12. *Remarks on Methods of Calculation.*

The processes of successive integration require a high degree of nominal accuracy throughout the work of calculation; otherwise the values that are obtained for  $I_n(0, 2)$  will diverge rapidly from the true values as  $n$  increases. Whatever be the degree of accuracy of  $p(x)$ , it is essential that there should be as exact a correspondence as possible between the adopted function and the calculations based on it. The difference between theoretical results and observations will then not be due to the method of calculation. The experience acquired in the present instance shows that when there are considerable irregularities in  $p(x)$  a great many values should be used in the numerical representation of the function. For values of  $x$  between 0 and 0.3, measured from the west end of the lake, as usual, it would have led to better results if considerably smaller intervals in  $x$  had been chosen. Values of  $p(x)$  at intervals of 0.002 in this region would have led to a large increase in accuracy. As it is, the values of  $I_n(0, 1)$  are certainly correct to 1 in 10,000, but this degree of accuracy is not sufficient for the higher roots of the period equation. For the first few values of  $n$  a much greater degree of accuracy is desirable.

There is nothing in the theoretical basis for the partition of the lake into western and eastern systems (see § 4) that requires the partition at  $x=1$ . It can be at any suitable value of  $x$ , and in the present case the division at  $x=0.3$  would have been better, as the value of  $p(x)$  is most irregular between  $x=0$  and  $x=0.3$ , the remaining portion being a smooth curve.

The method of solution of the problem, as expounded in §§ 2-4, is due to Professor J. PROUDMAN, and this paper is simply an application of his method. The calculations were begun by R. BALDWIN, and a graphical method of integration was used: his results indicated the need for a much greater degree of accuracy. The work

was then undertaken by A. T. DOODSON, who prepared the table of  $p(x)$  and initiated the method of calculation as described in the paper; the integrations were carried out chiefly by R. M. CAREY, and the rest of the work, together with the exposition as given here, was performed by A. T. DOODSON.

Throughout, the authors have experienced much assistance from Professor PROUDMAN, and they desire to express their thanks to him. They also desire to record their thanks to Dr E. M. WEDDERBURN for the data provided by him, and for the help and suggestions received from him.

TABLE I.  
*Lake Geneva Measurements.*  $u = 1.7052 \times 10^6$ .

Line.	South End.		North End.		Mid-point.		$\frac{ub(x)}{5 \times 10^5}$ .	$\frac{u^2 A(x)}{5 \times 10^{10}}$ .	$\frac{u^3 p(x)}{10^{15}}$ .	$s$ .
	Lat.	Long.	Lat.	Long.	Lat.	Long.				
1	46° 12'9"	3° 50'4"	46° 13'3"	3° 49'1"	46° 13'1"	3° 49'7"	·370	·0197	·0183	·0071
2	13·9	51·3	14·5	49·0	14·2	50·1	·617	·1493	·230	·0273
3	15·2	51·5	15·7	49·5	15·5	50·5	·546	·1742	·238	·0507
4	15·6	51·6	16·3	50·1	16·0	50·8	·478	·1455	·174	·0583
5	16·1	52·6	17·2	50·0	16·6	51·3	·776	·2224	·432	·0730
6	16·4	52·9	18·0	50·3	17·2	51·6	·885	·3101	·686	·0870
7	17·3	53·9	18·8	51·2	18·0	52·5	·895	·4072	·911	·1175
8	18·2	54·4	19·2	51·7	18·7	53·0	·777	·3527	·685	·1366
9	19·5	55·3	20·1	52·3	20·0	53·8	·835	·3923	·819	·1752
10	20·7	56·5	21·8	53·2	21·2	54·8	·931	·3401	·792	·2189
11	21·5	57·1	23·2	54·8	22·3	53·0	·899	·4219	·948	·2554
12	22·1	58·5	23·8	56·5	23·0	57·5	·791	·3422	·677	·2875
13	22·3	4° 0'0"	25·3	57·3	23·8	58·7	1·310	·5750	1·883	·3235
14	22·2	0·8	25·8	58·2	24·0	59·5	1·492	·8211	3·065	·3517
15	20·5	3·0	26·8	59·3	23·7	4° 1'1"	2·520	1·6927	10·668	·4198
16	21·8	5·8	27·9	4° 2'6"	24·8	4·2	2·456	2·8707	17·633	·6081
17	22·6	8·4	28·1	5·0	25·3	6·7	2·228	3·4481	19·207	·7374
18	24·3	10·2	28·7	7·6	26·5	8·9	1·800	3·3114	14·901	·8601
19	23·7	12·7	31·0	10·3	27·3	11·5	2·768	4·9460	34·225	·9968
20	23·9	13·8	30·5	12·6	27·2	13·2	2·464	5·2897	32·58	1·0903
21	24·2	16·2	31·1	15·3	27·6	15·8	2·596	5·5438	35·98	1·2348
22	24·4	19·3	30·3	19·9	27·3	19·6	2·210	5·5256	30·53	1·4360
23	24·7	23·5	29·4	24·1	27·1	23·8	1·830	4·3035	19·69	1·6187
24	24·1	25·6	28·5	27·4	26·3	26·5	1·695	3·6954	15·66	1·7317
25	23·7	28·2	27·5	30·5	25·6	29·3	1·539	2·7796	10·70	1·8353
26	23·3	29·4	27·2	31·2	25·2	30·3	1·505	2·2963	8·64	1·8848
27	23·3	30·6	26·9	31·9	25·1	31·2	1·386	1·4072	4·88	1·9204
28	23·6	31·9	26·5	33·1	25·0	32·5	1·104	·9257	2·555	1·9457
29	23·8	32·9	25·8	34·5	24·8	33·7	·860	·5643	1·212	1·9603
30	23·8	34·2	24·8	35·7	24·3	35·0	·522	·2134	·278	1·9948
31	23·7	35·2	23·7	35·2	23·7	35·2	·000	·0000	·000	2·0000

The latitude and longitude (east of Paris) of the terminal points and of the mid-points of the transversals drawn by WEDDERBURN on the map of Geneva are given above. The value of  $b(x)$  is the breadth of the lakes,  $A(x)$  is the area of the transverse section, and  $p(x)$  is the product; these quantities are expressed in lake units.

TABLE II.

*Values of  $p(x)$  for  $x=0$  to  $x=1$ , Western System.*

$x$ .	$\frac{w^3 p(x)}{10^{15}}$								
.01	.075	.21	.800	.41	9.60	.61	17.70	.81	16.98
.02	.148	.22	.792	.42	10.65	.62	17.90	.82	16.47
.03	.208	.23	.820	.43	11.38	.63	18.08	.83	15.97
.04	.230	.24	.875	.44	12.00	.64	18.25	.84	15.50
.05	.205	.25	.945	.45	12.55	.65	18.42	.85	15.10
.06	.243	.26	.945	.46	13.06	.66	18.59	.86	14.90
.07	.380	.27	.850	.47	13.50	.67	18.74	.87	15.10
.08	.562	.28	.708	.48	13.91	.68	18.87	.88	15.88
.09	.730	.29	.680	.49	14.29	.69	18.98	.89	17.50
.10	.860	.30	.750	.50	14.65	.70	19.08	.90	19.65
.11	.918	.31	1.000	.51	15.00	.71	19.15	.91	21.80
.12	.895	.32	1.575	.52	15.34	.72	19.20	.92	23.85
.13	.770	.33	2.150	.53	15.67	.73	19.22	.93	25.78
.14	.662	.34	2.550	.54	15.97	.74	19.20	.94	27.55
.15	.648	.35	2.975	.55	16.25	.75	19.12	.95	29.18
.16	.690	.36	3.500	.56	16.52	.76	18.98	.96	30.63
.17	.795	.37	4.250	.57	16.78	.77	18.73	.97	31.88
.18	.878	.38	5.300	.58	17.02	.78	18.38	.98	32.90
.19	.880	.39	6.750	.59	17.25	.79	17.95	.99	33.70
.20	.845	.40	8.250	.60	17.48	.80	17.48	1.00	34.25

TABLE III.

*Values of  $p(x)$  for  $x=0$  to  $x=1$ , Eastern System.*

(The value of  $x$  in the western system is the excess of 2 over the eastern value of  $x$ .)

$x$ .	$\frac{w^3 p(x)}{10^{15}}$								
.01	.42	.21	12.92	.41	20.88	.61	30.42	.81	35.50
.02	.87	.22	13.44	.42	21.29	.62	30.93	.82	35.22
.03	1.35	.23	13.97	.43	21.72	.63	31.43	.83	34.88
.04	1.85	.24	14.47	.44	22.15	.64	31.91	.84	34.51
.05	2.39	.25	14.93	.45	22.58	.65	32.38	.85	34.12
.06	3.05	.26	15.36	.46	23.02	.66	32.84	.86	33.73
.07	3.85	.27	15.75	.47	23.47	.67	33.29	.87	33.38
.08	4.82	.28	16.10	.48	23.93	.68	33.72	.88	33.05
.09	5.98	.29	16.45	.49	24.40	.69	34.12	.89	32.80
.10	7.24	.30	16.80	.50	24.87	.70	34.48	.90	32.65
.11	8.28	.31	17.15	.51	25.35	.71	34.82	.91	32.60
.12	8.89	.32	17.49	.52	25.83	.72	35.12	.92	32.67
.13	9.35	.33	17.83	.53	26.32	.73	35.39	.93	32.87
.14	9.73	.34	18.18	.54	26.82	.74	35.61	.94	33.17
.15	10.13	.35	18.55	.55	27.33	.75	35.79	.95	33.57
.16	10.54	.36	18.93	.56	27.84	.76	35.90	.96	34.02
.17	10.97	.37	19.31	.57	28.36	.77	35.95	.97	34.42
.18	11.43	.38	19.69	.58	28.88	.78	35.94	.98	34.59
.19	11.91	.39	20.08	.59	29.40	.79	35.87	.99	34.55
.20	12.41	.40	20.48	.60	29.91	.80	35.72	1.00	34.25

TABLE IV.

*Values of  $\kappa^{-n}I_n(0, x)$ , Western System.*

$x$ .	$n=1$ .	2.	3.	4.	5.	6.	7.	8.	9.
0.1	.0734	.0174	.0020	.0001					
0.2	.2990	.1460	.0356	.0052	.0005	.00004	.000002		
0.3	.7454	.6219	.2582	.0642	.0107	.00128	.000116	.000008	.0000005
0.4	1.4316	1.6690	.9475	.3162	.0696	.01090	.001281	.000118	.0000087
0.5	2.1795	2.9210	1.8636	.6919	.1686	.02915	.003778	.000382	.0000311
0.6	2.9586	4.3083	2.9605	1.1831	.3106	.05791	.008101	.000883	.0000776
0.7	3.7688	5.8484	4.2802	1.8276	.5140	.10287	.015459	.001813	.0001712
0.8	4.6123	7.5683	5.8794	2.6773	.8054	.17267	.027815	.003499	.0003540
0.9	5.4978	9.5307	7.8780	3.8387	1.2395	.28572	.049522	.006703	.0007298
1.0	6.4240	11.7405	10.3037	5.3519	1.8445	.45376	.083874	.012096	.0014015

TABLE V.

*Values of  $\kappa^{-n}I'_n(0, x)$ , Western System.*

$x$ .	$n=1$ .	2.	3.	4.	5.	6.	7.	8.	9.
0.1	1.4870	.5055	.0764	.0066	.0004				
0.2	3.2041	2.4616	.8140	.1497	.0176	.0015	.00010		
0.3	5.9889	8.0730	4.6600	1.4880	.3019	.0424	.00441	.000356	.000023
0.4	7.3034	11.8457	8.3358	3.2639	.8183	.1431	.01854	.001856	.000149
0.5	7.6381	13.1760	10.0068	4.2804	1.1788	.2273	.03250	.003592	.000317
0.6	7.9438	14.5998	12.0030	5.6065	1.6910	.3573	.05592	.006759	.000651
0.7	8.2620	16.2439	14.4794	7.3659	2.4191	.5556	.09435	.012349	.001286
0.8	8.6203	18.2498	17.6866	9.7886	3.4900	.8679	.15926	.022486	.002522
0.9	9.0967	21.0726	22.4506	13.6091	5.2917	1.4303	.28456	.043470	.005269
1.0	9.4035	22.9944	25.8675	16.5171	6.7554	1.9182	.40085	.064320	.008187

TABLE VI.

*Values of  $\kappa^{-n}I_n(0, x)$ , Eastern System.*

$x$ .	$n=1$ .	2.	3.	4.	5.	6.
0.1	.00979	.00032	.000005	.0000001		
0.2	.03415	.00195	.000056	.0000010	.00000001	
0.3	.07284	.00605	.000254	.0000064	.00000010	.0000000010
0.4	.12756	.01407	.000785	.0000264	.00000059	.0000000088
0.5	.19979	.02769	.001942	.0000821	.00000231	.0000000452
0.6	.29006	.04854	.004108	.0002096	.00000713	.0000001714
0.7	.39841	.07812	.007743	.0004626	.00001846	.0000005231
0.8	.51516	.11819	.013446	.0009223	.00004228	.0000013814
0.9	.67238	.17175	.022206	.0017334	.00009053	.0000033780
1.0	.84389	.24352	.035646	.0031541	.00018698	.0000079277

TABLE VII.

*Values of  $\kappa^{-n}I'_n(0, x)$ , Eastern System.*

$x$ .	$n = 1$ .	2.	3.	4.	5.	6.
0.1	.17988	.00842	.000178	.000002		
0.2	.31238	.02649	.001015	.000022	.0000003	
0.3	.46390	.05789	.003242	.000102	.0000020	.00000003
0.4	.63316	.10544	.007874	.000332	.0000089	.00000016
0.5	.87219	.16974	.015912	.000842	.0000286	.00000066
0.6	.99317	.24961	.028165	.001795	.0000735	.00000208
0.7	1.17414	.34481	.045509	.003396	.0001627	.00000540
0.8	1.36394	.46121	.070083	.006022	.0003321	.00001272
0.9	1.58847	.61907	.108107	.010662	.0006741	.00002960
1.0	1.84296	.82141	.163192	.018270	.0013098	.00006522

TABLE VIII.

*Values of Elevation.*

(These values have to be multiplied by a simple harmonic function of the time.)

$x$ .	Uninodal oscillations.	Binodal oscillations.
0.0	- 1.0000	- 1.000
0.05	- .8732	- .490
0.1	- .7358	- .055
0.2	- .4758	+ .375
0.3	- .1251	+ .460
0.4	+ .0114	+ .377
0.5	+ .0372	+ .328
0.6	+ .0560	+ .277
0.7	+ .0720	+ .222
0.8	+ .0868	+ .158
0.9	+ .1036	+ .077
1.0	+ .1126	+ .028
1.1	+ .1194	- .014
1.2	+ .1255	- .055
1.3	+ .1308	- .093
1.4	+ .1360	- .132
1.5	+ .1393	- .154
1.6	+ .1464	- .221
1.7	+ .1515	- .268
1.8	+ .1560	- .313
1.9	+ .1601	- .355
2.0	+ .1657	- .416

XXVI.—On Old Red Sandstone Plants showing Structure, from the Rhynie Chert Bed, Aberdeenshire. Part III. *Asteroxylon Mackiei*, Kidston and Lang. By R. Kidston, LL.D., F.R.S., and W. H. Lang, D.Sc., F.R.S., Barker Professor of Cryptogamic Botany in the University of Manchester. (With Seventeen Plates.)

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#### INTRODUCTION.

*Asteroxylon Mackiei* was a plant of more complicated organisation and larger size than either *Rhynia* or *Hornea*, which have been described from the silicified peat-bed at Rhynie in the two preceding papers of this series.\* The generic name refers to the stellate outline of the xylem of the stem as seen in cross section, while the specific name commemorates the original discovery of the plant remains by Dr MACKIE.†

The remains of *Asteroxylon*, though abundant, are unfortunately fragmentary, and caution is therefore necessary in mentally reconstructing the plant as it grew. The descriptions in this paper, though grouped as naturally as possible, are founded on isolated portions of a plant of considerable size. A large number of sections of the chert containing *Asteroxylon* have been examined, and there is reason to believe that the chief facts have been ascertained. While, however, we have a fuller knowledge of *Asteroxylon* than of most extinct plants, any fortunate block of the chert may supply data to complete or qualify the account given here. In anticipation of this, care has been taken to keep the statement of our observations as objective as possible. The mutual relations of the parts, and the probable habit of the plant, will be discussed at the close of the descriptive portion of the paper.

*Asteroxylon* was first seen in a few loose blocks of the chert discovered by Dr MACKIE. It has since been found in specimens taken from the section of the bed exposed *in situ* by Mr DAVID TAIT, and represented on p. 762 of Part I. Remains of *Asteroxylon* have been met with in the upper portion of the bed labelled A' 1, in bed A' 2, and in the upper six inches of bed B. The other blocks of the chert containing *Asteroxylon* have been found loose.

The most abundant and generally distributed parts are shoots of various sizes, the stem bearing numerous leaves. The central cylinder of these stems had a solid xylem, which was star-shaped in cross section, and gave off small leaf-traces from

\* *Trans. Roy. Soc. Edin.*, vol. li, p. 761, and vol. lii, p. 603.

† MACKIE, W., "The Rock Series of Craigbeg and Ord Hill, Rhynie, Aberdeenshire," *Trans. Edin. Geol. Soc.*, vol. x, pp. 205-236, pl. xxiii.

the enlarged ends of the rays. This construction was shown in the single figure published, without description, in Dr MACKIE'S paper.\* The structure of the branched shoot-system was primary throughout, no indication of secondary thickening having been found even in the largest stems. In addition to the leafy shoots, leafless cylindrical axes with a simpler type of central cylinder are met with. These rhizomes constituted the subterranean region of *Asteroxylon*. Their finer branches behaved like roots, while the transition between the larger rhizomes and the leafy shoots can be clearly followed. There is conclusive evidence, both from continuity and from the histology, that the rhizomes, with their fine root-like branches and the leafy shoots, were parts of the one plant, *Asteroxylon Mackiei*, the vegetative organs of which are thus pretty fully known.†

In two loose blocks of the chert small axes of a peculiar type have been found closely associated with the typical remains of the vegetative organs of *Asteroxylon*. In one of the blocks there were in addition dehiscent sporangia containing cuticularised spores. We regard these structures as possibly, or probably, constituting the fertile portion of *Asteroxylon*. Their description will therefore be given in this paper before the general discussion of the morphology of the plant, although in the absence of evidence of continuity or histological identity these interesting remains must be treated to some extent independently.

The various parts mentioned above will now be described. It will be convenient to deal in order with the leafless rhizomes, the transition from these to the leafy shoots, the shoots of various sizes, and lastly with the peculiar axes and the sporangia associated with them.

#### RHIZOMES.

The leafless axes of various sizes which are met with among the other remains of *Asteroxylon* have a broad cortex and a central cylinder consisting of a simple central strand of xylem surrounded by a wide zone of phloem. While the behaviour, especially of the finer branches, is very root-like, the axes with this type of construction, whatever their size, will be spoken of as rhizomes. The main reason for this is that, as will be seen in the next section, a gradual transition can be traced between certain of the leafless axes and the leafy shoots. Since some of the leafless axes were thus undoubtedly rhizomes, and no clear distinction can be drawn between these and the more root-like specimens, they seem best regarded as parts of a rhizome-system something like that of the existing Psilotales.

The mode of occurrence of the rhizomes at places in the upper part of bed A" 1

\* MACKIE, W., "The Rock Series of Craigbeg and Ord Hill, Rhynie, Aberdeenshire," *Trans. Edin. Geol. Soc.*, vol. x, pp. 205-236, pl. xxiii, fig. 6.

† It may assist the reader in forming an idea of the vegetative organs of *Asteroxylon* if we note at the outset the parallel afforded by the Psilotaceae, in which the plant has a leafless, cylindrical, subterranean rhizome of simple structure, certain branches of which pass into the more complex aerial leafy shoots. There are also resemblances in structure between the leafy shoot of *Asteroxylon* and that of the Psilotaceae, but the most helpful parallel as regards the anatomy is found in some species of *Lycopodium*.

is particularly interesting. In some blocks of the chert from this region a dark sandy band enclosing large stems and rhizomes of *Asteroxylon* overlies a clear peat composed of *Hornea* and *Rhynia major*. Rhizomes of *Asteroxylon* extend downwards in a root-like fashion into the upper portion of the clear peat, sometimes penetrating the portions of plants in it. It appears that, in this region at any rate, we have *Asteroxylon* preserved where it grew in the peat. It is clear that the rhizomes were the underground parts of the plant, and behaved physiologically like a root-system. This is further shown by the frequent intrusion of these axes into other rhizomes and into stems of *Asteroxylon* itself.

A general view of a section showing large stems of *Asteroxylon* embedded in the dark sandy matrix overlying clear peat is given in Pl. I, fig. 1. In the corresponding section given in fig. 2, the sandy band above contains stems of *Asteroxylon* and a rhizome *a* cut transversely. Two more slender rhizomes, at *b*, extend downwards through the underlying peat, which is composed of more or less decayed *Hornea* and *Rhynia major*. One of these rhizomes of *Asteroxylon* has grown through a rhizome of *Hornea* in the peat. The larger rhizome of *Asteroxylon* at *a* in the layer above contains a similar intrusive rhizome. This behaviour, which is also shown in the specimen in fig. 4, recalls a common appearance in rootlets of *Stigmaria*.

Intrusive rhizomes of small size have been frequently met with in the stems of *Asteroxylon*, and at first suggested comparison with the endogenous roots enclosed in the cortex of some species of *Lycopodium*. This interpretation was, however, negated by their obvious intrusion in some cases, while in others they were situated in the centre of the stele. In fig. 3, two stems of *Asteroxylon* are shown enclosed in a sandy matrix. In the cortex of the large stem above, a small rhizome is cut transversely at *a*. Another rhizome of similar size (*b*) is cut longitudinally as it lies free in the matrix. This rhizome passes right across the cortex of the stem, which occupies the lower portion of the figure.

The largest rhizomes were more than 5 mm. in diameter (fig. 4), and all sizes have been met with down to below 1 mm. (fig. 14). A remarkable feature, which holds for the rhizomes of all sizes, is the complete absence of absorbent hairs. In well-preserved specimens the surface is bounded by a smooth and continuous epidermis, but this has frequently broken down and disappeared.

A general idea of the range in size and structure of the rhizomes will be gathered from the examples figured on Pls. I, II, and IV. In the most clearly differentiated specimens it is possible to distinguish the epidermis (*ep.*), a narrow zone of outer cortex (*o.c.*), a zone of inner cortex (*i.c.*), which in the larger rhizomes is relatively broad, a clear zone of phloem (*ph.*), and the central strand of xylem (*x.*).

These regions are all shown in a transverse section of a fairly large rhizome which was figured in Part I (Pl. X, fig. 75), under the mistaken idea that it belonged to *Rhynia*. The general correspondence in construction with the stem of *Rhynia* is brought out by the mistake, which is now corrected.

The examples figured may now be briefly described.

The large rhizome in fig. 4 is slightly flattened, but must have been about 6 mm. in diameter. Growing within it is another about 3.5 mm. thick, and in the cortex of this are two small specimens under 1 mm. thick. The xylem is evident in all the rhizomes, and in the two larger specimens the zone of phloem around it is clearly marked. The inner and outer cortex can be distinguished in the largest rhizome, but the epidermis had almost completely broken down.

A specimen of medium size, with the stele divided preparatory to branching, is represented in fig. 5, and a similar dichotomy in obliquely longitudinal section in fig. 7. The longitudinal section in fig. 6 is of a rhizome of about the same size. The strand of xylem is only followed for a short distance, but the section is otherwise truly longitudinal. The surface is smooth, the epidermis is intact and well preserved, the outer and inner cortex can be distinguished, and the phloem is fairly well marked.

In the small rhizomes (figs. 8, 9, 14, 26-29) the same regions can be distinguished as in the larger specimens, but this is not always evident without close examination. Thus in fig. 29 the epidermis is wanting, but the regions are fairly well marked, and they can also be readily distinguished in fig. 26. In fig. 9 the epidermis is wanting, the outer cortex is about two cells deep; there is a very narrow zone of inner cortex and a fairly wide zone of phloem, but the limit between these tissues is difficult to distinguish. The junction of inner cortex and phloem is clearer in fig. 14. The epidermis is present on the small specimen in fig. 27. The transverse section on the left in fig. 28 is interesting, since on part of its circumference the epidermis is persistent and the surface smooth, while on the other side the epidermis has broken down.

Rhizomes of all sizes evidently branched repeatedly. The most usual method seems to have been equal or dichotomous branching, as is shown in figs. 5 and 7. In other specimens there are indications that the branching was unequal or lateral. It seems always to have been exogenous, and in favourable cases the epidermis has been traced from a main axis to a branch.

The examples of rhizomes described above were all cylindrical. It should be mentioned that some other sections have shown a more irregular outline, and included several steles. There is nothing to suggest, however, that they were anything but cases of irregular subdivision of the rhizome, such as are met with in *Psilotum*.

The details of structure of the rhizomes can be dealt with briefly, since the histology of some of the more important tissues will be more fully considered in relation to other parts of the plant. There are, however, some features peculiar to these underground parts.

The epidermal cells are smaller and shallower than those of the outer cortex (figs. 6, 27, 28). They are well shown in the longitudinal sections of the outer

tissues of large rhizomes in figs. 12 and 13. In many specimens, as already mentioned, the epidermis has broken down, the surface thus losing the smooth appearance (fig. 29).

The zone of outer cortex is usually well marked in the larger rhizomes, where it consists of some five or fewer layers of rather large cells which form a relatively persistent zone usually free from fungal hyphæ (figs. 12 and 13). In the smaller and more root-like rhizomes the outer cortex is still clearly recognisable, but may be reduced to one or two layers.

The inner cortex (figs. 13 and 29) is composed of narrower and more delicate cells. It is often more or less broken down, and frequently contains a particular fungus, which is usually wanting in the outer cortex on the one hand and the phloem on the other. The same features characterise this region in the small rhizomes, where it may be reduced to one or two layers of cells, and be difficult to distinguish from the phloem unless the fungus be present.\*

The phloem persists, and is fairly well preserved in many of the rhizomes. In the larger examples (fig. 4) it forms a broad, clear zone of closely associated elements, all of one kind. Even in the smallest rhizomes it is usually distinguishable (fig. 14). The elements composing it, which are elongated tubes with pointed or transverse ends, will be described in the next section in connection with the transition region which has supplied the best-preserved examples (*cf.* figs. 20 and 22).

The xylem in rhizomes of all sizes forms a simple, more or less cylindrical, strand of tracheides, with no indication of a distinction between protoxylem and metaxylem. All the tracheides have the peculiar type of spiral thickening characteristic of *Asteroxylon*. This feature is shown in figs. 10 and 11, which are details from the rhizomes in figs. 8 and 6 respectively. It will be described in connection with the leafy stems.

#### TRANSITION REGION FROM RHIZOMES TO LEAFY SHOOTS.

A series of intermediate stages has been traced between the characteristic structure of the rhizome, as described in the preceding section, and that of the leafy shoot of *Asteroxylon*. It has not as a rule been found possible to follow the changes in a series of sections of one specimen, but the intermediate grades are so completely represented as to leave no doubt as to the reality of the transition.

The transition is indicated by a number of changes shown in different degrees by the various specimens. As compared with that of the rhizome, the epidermis becomes more distinct and definite, and has thicker external walls. The cortex,

\* The question as to the saprophytic or possible mycorrhizal nature of this fungus is deferred to Part IV, in which the fungi present in the peat-bed will be considered.

while retaining the simple contrast of a narrow outer and a broad inner zone, often appears more definite and better preserved. The central xylem becomes stellate in cross section, thus intruding into the wide zone of phloem. Scale-leaves appear on the surface. These sometimes have leaf-traces in relation to them, but may be borne on a region of the stem with no leaf-traces.

The general features will be evident from the specimens represented in figs. 15-25 and fig. 95. Some of these examples will now be referred to and described.

In the portion of clear peat included by fig. 15 there are to be seen a rhizome of medium size cut in obliquely longitudinal section, and below this a transverse section of an axis with the characters of the transition region. The general correspondence in structure between them will be evident at a glance. The xylem strand of the transition region is damaged, but is surrounded by a broad zone of phloem, and is not giving off any leaf-traces, and none are present in the cortex. This is differentiated into a broad inner cortex and a narrow zone of outer cortex. The epidermis has broken down around part of the circumference, but is very distinct on the other part. Here the outline is irregular, owing to projections which comparison with other specimens shows to be scale-leaves. A small intrusive rhizome is to be seen in the cortex on the lower side of the figure.

The longitudinal section shown in fig. 16 has also essentially the same structure as the rhizome, and may be compared with fig. 6. It differs in the strongly developed epidermis and cuticle, the indications of scale-leaves (*sc.l.*), and the presence of a few leaf-traces, one of which is shown at the lower part of the figure at *l.t.* The cortex, which is rather broken down, shows outer and inner zones. The stele is of the type characteristic of the rhizome, with a broad zone of exceptionally well-preserved phloem (*cf.* fig. 22) around the large but simple strand of xylem.

The two axes, still connected as they have arisen by branching, in fig. 25 show a similarly simple structure in transverse section, while the smaller axis above is in a more advanced stage of transition, with an angled xylem giving off leaf-traces.

Successive stages of the transition from different specimens are seen in figs. 17, 18, 19, and 24. The specimen in fig. 17 hardly differs from a rhizome, except in the distinctness of the epidermis. There are no leaf-traces or indications of scale-leaves. The stele of this axis, which is to be regarded as in an early transition stage, has just given off a small lateral branch. The transverse section in fig. 18 shows the small scale-leaves very well. No leaf-traces are passing out to them, but the xylem of the stele is distinctly angled. This is still more marked in the small stem in fig. 25, in which a leaf-trace is departing from one angle of the quadrangular xylem. The stem represented in fig. 19 is preparing to branch, and contains two steles. The xylem of these has projecting rays, which extend nearly to the limit between the phloem and inner cortex. This stem bears scale-leaves, and, in relation

to these, small leaf-traces are given off from the angles of the xylem. A scale-leaf from another specimen is more highly magnified in fig. 23.

In the stem represented in fig. 24 the stele has all the features to be described below for the large leafy stems, but the cortex is of the simpler type, and the leaves appear to have been small and scale-like. The large specimen on Pl. XIII, fig. 95, is better preserved, but its construction is at about the same grade of complexity.

In the details of its histology the transition region is intermediate between the rhizomes and the leafy shoots, but more like the former. Only special features, or those tissues that are particularly well shown in this region, need be mentioned. The tissues are brought out most clearly in fig. 20, which is a transverse section of an early transition region from the same axis as fig. 17; in fig. 22, which is a portion of the longitudinal section in fig. 16, and is also of the early transition region; and in fig. 21, which is a portion of the late transition region shown in fig. 19.

The epidermis is usually well preserved, and its small cells covered with cuticle form a more definite boundary than on the rhizome (fig. 20, *ep.*). Stomata were present in it (fig. 73). The outer and inner cortex resemble the corresponding tissues of the large rhizomes, and, as fig. 20 shows, may be very well preserved. The inner cortex is often infested with the same fungus as that occurring in the rhizomes (figs. 20 and 22).

The xylem calls for no special description, except to note that when it becomes stellate in the more advanced transition region the rays from which the leaf-traces depart are composed, in some cases at least, of narrower tracheides.

The phloem has tended to persist, and some of the best-preserved examples of this tissue are supplied by the transition region. It consists of closely associated elements, all of one kind (figs. 20 and 21). In longitudinal section (fig. 22) these appear as elongated tubular cells, which sometimes fit together with pointed ends, and at other times have transverse end-walls.

In the less advanced specimens of the transition region the phloem, as in the rhizome, forms a broad, clear zone around the more or less cylindrical xylem. As the latter becomes stellate its projecting rays divide up the zone of phloem, but do not reach to the periphery of this. There is thus phloem between the rays of xylem and also forming a narrow zone outside the rays (fig. 21). The xylem of a leaf-trace passing out to the scale-leaves is surrounded by a sheath of this outer zone of phloem (fig. 21, *lt.*)

#### THE LEAFY SHOOT.

Leafy shoots ranging in diameter from 1 centimetre to 1 millimetre (*cf.* figs. 96 and 30) form the most abundant material of *Asteroxylon* met with in those portions of the chert that have been examined. The structure in the large as in the small specimens is primary, and was determined once for all in development. The

differences in size are best explained by the fragments coming from different positions in a branch-system. Along with the difference in size there is naturally some in the details of the structure, but a common plan of construction holds throughout. This will be evident in comparing the specimens figured on Pls. VI and VII.

Since the shoots in the material examined are represented by short fragments, no general picture of the branch-system can be obtained. Examples of the branching, which in most cases was lateral, will be described later.

The stem bore numerous leaves of relatively small size, so that the general form of the plant must have depended on the branching. The first leaves on the transition region from the rhizome have been seen to be small scales (figs. 18, 19, 23, and 95), sometimes without any leaf-traces in connection with them, and at other times with a small trace extending to the base of the leaf. The leaves on the aerial shoots are larger, but their leaf-traces also never extend into the free portions, ending in the enlarged leaf-bases (fig. 35). The long simple leaves are seen attached to the stem in the longitudinal sections represented in figs. 31 and 32. They are met with cut across, around many of the transverse sections of stems (figs. 96 and 46). These and other sections also show the projecting leaf-bases, while in fig. 33 the leaves are just separating from the stem. While the leaf-bases on the stem include the ends of the leaf-traces, the sections of the free portions of the leaves have never shown any indication of the presence of a vascular bundle, however well preserved the tissues may be (*cf.* figs. 96 and 37). Fig. 36 shows the leaves closely crowded, and so arranged as to suggest that the section has passed across a bud. On the stems the leaves were more or less closely placed, and, as the arrangement of the leaf-traces shows, were borne spirally. A leaf lying free in the matrix is shown in fig. 38, while others are cut so as to show the stomata in fig. 40. Fig. 30 is a cross section of a very small twig, with the closely placed leaves around it. In cross section the leaves were oval, being thus slightly dorsiventral.

The arrangement of the tissues in the stem is most clearly brought out in transverse section. A survey of the figures on Pls. VI, VII, and XIII will show the features mentioned in the following general description, which is based on the better-preserved examples of large or medium size.

The surface of the stem and leaf-bases is bounded by an epidermis (*ep.*). This has a well-marked cuticle, which is often traceable as the limit of the stem when the epidermal cells are unrecognisable. Within the epidermis is a narrow zone of outer cortex (*o.c.*). The inner cortex (*i.c.*) is sometimes uniform, but is usually differentiated into outer, middle, and inner zones (*i.c.o.*, *i.c.m.*, *i.c.i.*). Only in the case of one stem has an endodermis-like layer (*en.*) been recognisable limiting the stele, which in all cases, however, is clearly contrasted with the cortex. The arrangement of the tissues in the stele has already been traced in the more advanced specimens of the transition region. The xylem (*xy.*) is stellate in cross section, and groups of

protoxylem elements (*px.*) are sometimes recognisable in the enlarged ends of the rays. The phloem (*ph.*) occupies the bays of the stellate xylem, and forms a narrow zone outside the ends of the rays of xylem (fig. 72); it is often more or less completely decayed.

Leaf-traces (*lt.*), consisting of a small centrarch strand of xylem surrounded by a zone of phloem, can be seen departing from the stele or on their way out to the leaf-bases. The much larger traces for the lateral branches (*br. tr.*) are occasionally met with, but, unlike the leaf-traces, pass out from the cortex of the stem into the branches.

Attention may now be directed to some of the figures in which particular features mentioned in the above general account are shown especially clearly.

The complete differentiation of a large stem is well shown in fig. 96, which will be referred to later in relation to the preparation for equal division exhibited by the stele. The corresponding tissues are labelled in the portions of other large stems in figs. 41 and 43. The epidermis is not evident, though the cuticle marks the limit of the stem. In the outer cortex (*o.c.*), which is light coloured owing to the disappearance of the cell-contents, some leaf-traces (*lt.*) are present. Within it the outer zone of the inner cortex (*i.c.o.*) is recognisable as a narrow and not very well characterised layer. The broad middle zone of the inner cortex (*i.c.m.*) is prominent owing to the trabecular arrangement of the cells with wide intercellular spaces between the rows. The coherent tissue around the stele, dark in fig. 41, is the inner zone of the inner cortex (*i.c.i.*). The stellate xylem (*xy.*), with the widened ends of the rays divided and enlarged, is well preserved. Leaf-traces (*lt.*) are present in relation to the rays. The phloem (*ph.*) between the rays of xylem has decayed and disappeared, while the narrow zone of phloem within the cortex and around the xylem is compressed, but recognisable.

The somewhat smaller stem in fig. 42 does not show the zoning of the decayed inner cortex, but the dark remains of the cell-contents have persisted in the outer cortex and render it prominent. The tissues of the leaf-bases and free portions of the leaves have a similar appearance. The stem in fig. 45 shows the zones of the cortex clearly. The stele has the massive four-rayed xylem well preserved, but the phloem has perished from between the rays.

Fig. 44 is of a stem of fair size, but with a less massive, rayed xylem. This and the smaller stem in fig. 46 have a similar zoning of the cortex to the larger stems, and have the outline irregular from the projecting leaf-bases. The still smaller stem in fig. 47 shows the trabecular middle zone of the inner cortex clearly, and has the xylem of the stele three-rayed. The cortex of the three small twigs associated together (fig. 48) has so completely decayed, that their outlines are only dimly traceable.

All the transverse sections of stems on Pl. VI are magnified 14 diameters, and are thus strictly comparable.

Two small twigs magnified 20 diameters are represented in fig. 54, and show the proportional size of the solid triangular or quadrangular strand of xylem and the stem itself better than those in fig. 48. The soft tissues are, however, very poorly preserved. The bays in the angled xylem are here shallow, and there is some reason to think that in some ultimate branches the xylem formed a cylindrical strand, though no well-preserved specimens of this have been seen (*cf.* the specimens in fig. 47, on the right).

The stem in fig. 49 is a good example of one in which the inner cortex is composed of uniform tissue with large intercellular spaces, and is not differentiated into zones. The narrow outer cortex is distinct from this. The obliquely cut stele is giving off large traces, one of which is probably for a branch and the other a leaf-trace.

The arrangement of the tissues in the stele has been briefly described above, and was evident in the figures of complete transverse sections of stems on Pl. VI. A number of steles are represented somewhat more highly magnified on Pl. VII, and show the details better. Thus fig. 50 is the stele of a small stem, with the xylem three-rayed, and the ends of the rays gradually widening. The phloem is fairly well preserved in the bays. Fig. 53 is a typical large stele as usually preserved. The ends of the four rays of the xylem are greatly expanded, and leaf-traces are departing from them. The phloem in the bays is only partially decayed, but that around the xylem has collapsed. This stele may be compared with the specimen in fig. 72, in which the phloem is exceptionally well preserved. The stele in fig. 57 shows only the xylem well, but this is of interest on account of the more slender three-rayed central portion which connects the widened and divided ends of the rays from which the small leaves-traces depart. In the stele in fig. 52 the central connecting portion of the xylem is imperfectly developed, and the numerous widened ends are partially isolated. In fig. 51 the well-preserved xylem of the stele is separated into distinct masses by the phloem extending across.

Before passing to consider histological details, mention must be made of some sections of the shoot in which the imperfect differentiation of the tissues suggests nearness to the apical region. The specimen represented in fig. 58 can only be interpreted as of this nature. It is an accurately transverse section of a twig, the outline of which is irregular owing to the projecting leaves. The tissues of these and of the epidermis and outer cortex, with which they are continuous, appear almost mature and of full thickness. The inner cortex, on the other hand, is narrow and immature, though it shows the distinction of zones. The stele is represented by the central clear area, with no indication of developed xylem, a tissue which in *Asteroxylon* is very persistent. The stele thus appears completely undifferentiated, and, unlike the cortex, does not show the cells clearly.

Fig. 59 is of a specimen of somewhat different character, and appears to belong to a leafy shoot of fair size. It bears leaf-bases, and the outer and inner cortex have

numerous leaf-traces cut across. The leaf-traces close to the periphery of the stele have well-developed xylem. The only other thickened elements are the poles of the stellate xylem, from which differentiation in the thin-walled tissue of the immature stele will proceed centripetally. This is more apparent in the next lower section of the same stele, which is more highly magnified in fig. 60. In this the poles of the imperfectly differentiated xylem, marked *x.*, are readily distinguishable from the leaf-traces. Figs. 59 and 60 are apparently of sections just below the apex, where the lignified leaf-traces are crowded and pursuing a more vertical course, while the stem-xylem is only beginning to be lignified.

The various tissues, the arrangement of which in transverse sections has been described, are of course found in longitudinal sections (fig. 63), but few good examples have been available for study. The longitudinal sections tend to be less satisfactory, since the preservation of the tissues in these shoots, though good up to a point, is by no means perfect. Owing, in part at least, to the effect of saprophytic fungi the cell-walls are often hardly to be traced, although the zones of tissue may be obvious. The difficulties arising from this imperfect preservation are especially felt in studying longitudinal sections of *Asteroxylon* (figs. 63 and 31).

In proceeding to deal with the various tissues in detail, the information obtained from longitudinal or oblique sections will be combined with that from the transverse sections.

The epidermis, as seen on the stem, leaf-bases, and leaves, is a single layer of cells, the outer walls of which are thickened, and covered with a distinct cuticle (figs. 61 and 62). The cuticle often persists when the rest of the cell-walls has disappeared. The outer walls of the cells may be flat or papillate (figs. 61 and 39). In surface view or tangential section the epidermal cells are somewhat longer than broad (fig. 65), and in some well-preserved specimens their outer walls have shown a median line similar to that in *Rhynia Gwynne-Vaughani* (Part I, Pl. VI, fig. 31). Stomata of ordinary form have been seen on the leaves, though even there they seem to be relatively few (fig. 40), and they occurred on the aerial stems also, as they did in the epidermis of the transition region (*cf.* fig. 73). A well-preserved stoma from the aerial shoot is represented in fig. 65, and another in vertical section in fig. 66. As the latter figure shows, the guard-cells were distinctly depressed below the general surface. The pore of the stoma on the aerial shoot was much smaller than on the transition region (*cf.* figs. 65 and 73).

The outer cortex is a narrow zone, some six cells deep. Its cells were tangentially extended, and are usually compressed (figs. 62 and 58). The contents of the cells may persist as a dark substance, making the region prominent (figs. 42, 62, and 58), or the contents may have disappeared and the zone appear clear (figs. 43 and 45). This applies to the contents of the epidermal cells also (figs. 61, 62, and 65).

The tissues of the leaves are continuous with the epidermis and outer cortex of

the stem. When the free portions of the leaves are well preserved (fig. 37) the thick-walled epidermis encloses a uniform tissue, with dark contents similar to the cortex. As already mentioned, no vascular tissue is present in the free portion of the leaf.

The wider inner cortex may be a uniform tissue (fig. 49), but it is usually differentiated into outer, middle, and inner zones (figs. 41 and 43). In the cases in which it is uniform the tissue has large intercellular spaces. When three zones are distinguishable, it is the middle zone that has the prominent intercellular spaces, and often shows a definitely trabecular arrangement of the rows of cells (fig. 67). The narrow collapsed cells between the intercellular spaces come out more clearly in fig. 71, though the trabecular arrangement is not shown in this specimen. Longitudinal sections show that the trabeculae were vertically extended plates, and not rows of cells. The outer zone beneath the outer cortex, and especially the wider inner zone around the stele, are composed of more compact tissue. The former is often ill-marked, while the inner zone is well characterised, and contrasts with the middle zone by reason of its closely associated small elements (figs. 67 and 68). While the cortical tissues show clearly the differences of the various zones, the cells have been so far altered in the process of decay as to make detailed description inadvisable. Longitudinal sections show that all the cells were somewhat longer than broad, and that those of the inner zone of the inner cortex were closely packed and more elongated. There is no evidence, however, to show that these latter elements were developed as fibres.

As a rule there is no prominent layer marking off the cortex from the stele, but in one large stem\* a well-marked layer in the position of an endodermis was so evident, that it cannot be passed over as without significance, although found in a single example only (fig. 69; *cf.* figs. 100 and 102). The soft tissues of the inner cortex and phloem of this stem were rather more than usually indistinct, though the zonation of the tissues was clear, and the layer of cells in question stood out between these two regions. Its cell-walls were prominent owing to their dark colour. The whole appearance suggests comparison with such an ill-defined endodermis as is met with in the stems of some species of *Lycopodium*.

The soft tissues of the stele, which have been termed collectively the phloem, occupied the bays and formed a narrow zone outside the arms of the xylem. As has been seen, they are usually badly decayed or compressed, and have often in great part disappeared, or been replaced by saprophytic fungi. In a few specimens of the leafy shoot they have been found well preserved. The more decayed examples must evidently be interpreted in the light of those better-preserved ones and of the sections of the transition region. It has been described above how, with the change from the circular to the stellate cross section of the xylem, the phloem of the stem can be clearly related to that of the rhizome.

\* This particular stem was undergoing branching of a peculiar endogenous type, as will be described below.

The large, thin-walled elements of the phloem were preserved in the small stele represented in fig. 50. The large stele in fig. 72 is the best example that has been met with. In this the phloem is complete, both in the bays and around the stele. No clear distinction can be drawn between the thin-walled tissue in these two regions. The elements in the centre of the bays are wider than those abutting on the xylem, and suggest a possible distinction of phloem proper and conjunctive parenchyma. It does not appear advisable, however, to attempt such distinctions of tissues on the specimens so far examined. The elements of the phloem with dark contents in fig. 72 have probably been cut across not far from the transverse end-wall.

The phloem in the stem is as a rule so much more decayed than in the rhizomes or transition region that it is better to rely on these (*cf.* fig. 22) for showing the structure in longitudinal section. An example from a stem is represented in fig. 70. The elements of phloem within the cortex are elongated and compressed. The wider elements from one of the bays are partially decayed. From this and other specimens it was clear that they were wide elongated tubes, which sometimes had the almost transverse end-walls to which attention has been directed in the case of the better-preserved phloem of the transition region.

It is convenient to select for the more detailed description of the xylem and of the structure of the tracheides examples in which the protoxylem was recognisable, but the fact that this was not always possible must be borne in mind. This is the case, for example, with the steles in figs. 50, 53, and 57, which may be contrasted with fig. 56, where the position of the immersed protoxylems comes out prominently.

Figs. 74, 75, and 76 represent three rays of the xylem of one large stele. There is here no difficulty in distinguishing from the larger tracheides making up the bulk of the xylem the groups of small and compressed tracheides (*px.*) within the ends of the rays but close to the surface. These small tracheides are the protoxylem, and they are here enclosed by the larger elements of the metaxylem. Sometimes a protoxylem group appears divided (fig. 75), and when a division is extending to the surface there is the preparation for the separation of a leaf-trace. The tracheides in figs. 74 to 76 are to some extent separated by the decay of the middle lamella. The apparently uniform thickening of the wall proves on careful examination to be the optical expression of a thin wall from which the localised thickening projects inwards, thus diminishing the cavity. There are none of the characteristics of a pitted wall in the transverse sections of the tracheides, either of the protoxylem or metaxylem.

The character of the thickening is evident when the tracheides are seen in longitudinal section (figs. 77 to 79). The wall of the tracheide is moderately thin, but has a spiral or irregularly spiral thickening. This projects into the cavity as rather thin flat ledges, which, when seen from above in the transverse section, gives the appearance of a uniformly thickened wall. The tracheides of the protoxylem (figs. 77 and 78, *px.*) are much narrower, and have spiral or annular thickening. The clear distinction of protoxylem and metaxylem, while the thickening of all the tracheides is spiral, is

characteristic. No trace of any scalariform or pitted tracheides has been seen. The tracheides were of considerable length, and had pointed ends.

The leaf-traces arise from the arms of the xylem, more than one vertical series coming from each arm, at least in the case of the large and medium-sized stems. This is shown in a number of figures, but the reader may be especially referred to the steles in figs. 53 and 57. The arrangement and relations of the leaf-traces to the stem-xylem are also well shown in figs. 55 and 56, in which the tissues other than the xylem are partially or wholly omitted owing to the screen used in taking the photograph.

The xylem of the larger leaf-traces, which often arose from steles in which the protoxylem was recognisable, shows a clear differentiation into small central tracheides (protoxylem) surrounded by larger metaxylem elements (figs. 80 and 81). These in suitable specimens could be seen to be respectively continuous with the protoxylem and metaxylem of the stem. The differentiation may be evident in the leaf-trace even when it cannot be traced into the stem xylem (fig. 82). It can be seen even in small traces, although in them the metaxylem elements often form an incomplete layer around the protoxylem.

The leaf-traces exhibit a considerable range in size which does not go strictly parallel with the size of the stems or steles. They are often larger, and sometimes hollow near the periphery of the stem, an appearance that is probably in part to be accounted for by changes occurring with age (fig. 43).

The xylem of the leaf-trace acquires a sheath of the soft tissues or phloem which surrounds the xylem of the stele. This appears according to the preservation as composed of more or less collapsed or decayed, elongated cells. The nature of this tissue in the leaf-trace and its continuity with the phloem of the stem is most clearly seen when the latter tissue is well preserved, as in the specimen from the transition region already described, which is represented in figs. 19 and 21.

The leaf-traces thus arising from the stele seem to have pursued an almost vertical course for some distance, and are therefore commonly met with in the immediate neighbourhood of the stele, and especially in the outer zone of phloem. This is seen in many of the transverse sections, and also in fig. 63. The leaf-trace seems to have been more oblique in its passage through the inner cortex, but on reaching the outer cortex it is again almost vertical, till it ends in the leaf-base. This is best shown in the obliquely longitudinal section in fig. 64.

#### BRANCHING OF THE SHOOT.

The shoot of *Asteroxylon* was evidently repeatedly branched, and a number of examples must be referred to and several types of branching distinguished. This is all that can be done, since the fragmentary nature of the remains is a disadvantage in the investigation of this feature of the plant. The type of branching most frequently met with is exogenous, and, as shown by the nature of the vascular

supply, clearly lateral. In a single remarkable example the lateral branch appeared to be endogenous. In addition to lateral branching, indications of dichotomy, both of large and small shoots, have been found.

The large stem in fig. 96 appears from the disposition of the tissues in the stele, where two distinct stellate xylems are enclosed in a common mass of phloem, to be preparing for dichotomous branching. It is the only specimen of the kind so far met with. There are other indications of the occurrence of dichotomy, however. Thus in the case of a lateral branch, to be described below, the series showed the continuation of the branch into two equal branches, although the actual division of the stele was not followed. The division had taken place at a level where the stele of the primary branch had not acquired the characteristically stellate xylem. It is significant that in some other examples, in which two equal steles have been found within the same cortex, the outlines of their xylems are suggestive of an early stage in the progression to the stellate type. There is, however, no direct evidence in these cases, one of which is represented in fig. 89, that we are dealing with an early dichotomy of a lateral branch.

Another region in which the branching may have been dichotomous was in the fine ultimate branches. These, however, are so ill preserved, that little can be said beyond drawing attention to the fact that their association is suggestive of such a mode of subdivision. The group of small twigs in fig. 48 may be compared with the smaller but equally decayed twigs on the right side of fig. 47.

The relations of lateral exogenous branches to the main stem have been more clearly followed in a number of examples. The lateral nature of the branch is shown not merely by its small size relatively to the main axis (figs. 86, 90, and 95), but by its vascular supply being derived from a cylindrical branch-trace separated from one arm of the stellate xylem. This trace is considerably larger than a leaf-trace, but, like it, takes a sheath of phloem as it separates from the stele. It passes more or less obliquely through the cortex of the main stem and enters the branch. In this it gradually assumes the characters of a stem-stele, the xylem becoming angled and stellate, and giving off leaf-traces to the leaves of the branch.

Examples of different stages in the process thus summarised may now be described and illustrated. In fig. 83 the separation of a branch-trace from one arm of the stellar xylem is seen in a moderately small stem. In fig. 84 a branch-trace is present well out in the cortex. Figs. 85, 86, and 87 form a series following a branch-trace from the outer cortex of a large stem (fig. 85) into a small branch, the stele of which rapidly assumes the characters of that of a leafy shoot, the xylem becoming stellate (figs. 86 and 87). The base of a small lateral branch still connected with the parent stem is shown in fig. 95, both axes being cut transversely. In figs. 90 and 91 the branch is standing at right angles to the parent stem, so that while the latter is cut transversely the branch is followed in longitudinal section. The further portion of the branch in fig. 91 is shown more highly magnified in

fig. 92. An interesting feature in connection with the lateral branching is the way in which the branch may remain connected to its main stem by a web-like flange of cortical tissue, as is shown by the example in fig. 88.

The general character of the branch-trace and its size relatively to the leaf-trace can be gathered from figs. 83 and 84. No protoxylem elements are distinguishable in any of the branch-traces that have been observed. As is more clearly shown by fig. 94, the xylem of the trace is surrounded by a zone of collapsed phloem.

A point of some interest is the more or less close parallel between the assumption by the branch-trace of the features of the stem-stele and the changes in the transition from the rhizome to the leafy shoot. In the examples of lateral branching figured the change is effected rapidly. A specimen has been met with, however, in which a branch on a leafy shoot maintained for more than a centimetre a broad, clear zone of phloem around the cylindrical strand of xylem of its stele. The base of another branch cut transversely in the tangential section of its parent stem is shown in fig. 93. The structure of the branch at this level resembles that of a rhizome, but soon passed, as succeeding sections of the series showed, into that characteristic of the transition region. This section at first suggested the lateral origin of a rhizome from a leafy shoot, but cannot by itself be taken as affording evidence of this.

A special account must be given of one case of branching which is remarkable for its being apparently endogenous. The large stem exhibiting it has already been referred to as the only specimen showing a well-marked layer in the position of an endodermis (p. 654); it occurred in the block containing the sporangia, to be described below. The stem can be traced unbranched through a number of sections of the series cut from this block. An enlargement of one arm of the xylem and a bulging out of the endodermis indicates the approach to the place of branching (fig. 97). As the large branch-trace separates and moves outwards it becomes evident that the cortex of the branch is continuous with the tissue within the endodermis of the main stem (fig. 98, and more highly magnified in fig. 100). This amounts to saying that the branch is endogenous. This conclusion is supported by the discontinuity between the superficial tissues of the main stem and the branch (fig. 100, X, and fig. 101). Such a type of branching of the shoot is, so far as we know, unique, both among living and extinct Vascular Cryptogams.

The cortex of this branch is continuous with that of two small stems, which in the lower sections of the series lay in the neighbourhood of the large stem. The whole series is consistent with the giving off of an endogenous lateral branch that bent back and divided equally. In the higher section figured in fig. 99 the stele of the curved branch is cut through twice, first at *br. tr.*, where the branch is emerging from the main stem, and again where it has divided into two steles within the one cortex (*Ba*, *Bb*) at a distance from this. In the section at a lower level (fig. 98)

the branch-trace (*br. tr.*) is cut in the neighbourhood of the parent stele, while the most distal part of the branch is shown divided into two (*Ba* and *Bb*) adjacent to the main stem, but not connected with it.

#### POSSIBLE FERTILE REGION OF ASTEROXYLON.

The parts so far described are shown by evidence of continuity, by the existence of intermediate grades, and by histological agreement to be the rhizomes, stems, and leaves of one plant. We have thus a fairly complete knowledge of the vegetative organs of *Asteroxylon Mackiei*.

We owe our knowledge of the structures that have now to be described entirely to two small blocks of chert, which were found loose. In sections of one of these a number of small axes of peculiar type, with single or paired steles (fig. 107), had been met with, associated with stems, leaves, and rhizomes of *Asteroxylon*, when Dr GORDON kindly sent us a section he had cut from another loose block of the Rhynie chert. He also sent us the block, which was cut into a series of sections.

We wish to express our indebtedness to Dr GORDON for this important addition to the material upon which this paper is based.

This block proved to be a bedded peat, free from sand, and largely made up of portions of the peculiar type of axis mentioned above. In the peat were a number of sporangia of a new type, and numerous scattered spores derived from them. The peculiar axes and the sporangia were associated with stems of *Asteroxylon* of various sizes, one large one showing the endogenous branching already described. There were also structures resembling the rhizomes of *Asteroxylon*. Some of these, unlike the other remains, tended to cross the bedding as if they had penetrated an already formed peat.

The appearance of the peat in the block we received from Dr GORDON, and especially the association with undoubted *Asteroxylon* of the peculiar axes that have to be described, will be gathered from the photographs on Pl. XV, figs. 102-106. The region in fig. 102 shows a large stem of *Asteroxylon* and some more or less well-preserved smaller stems. The peat in the lower portion of the figure is made up of the peculiar axes, and the track of a perished rhizome of *Asteroxylon* is traceable obliquely across the bedding. Fig. 104 shows a fairly large stem of *Asteroxylon* below, while the peat above is made up of a mixture of the peculiar axes and of rhizome-like branches of *Asteroxylon*, or of isolated strands of xylem composed of the characteristic tracheides of this plant. In fig. 103 the branching structure has all the features of a root-like rhizome of *Asteroxylon*. It is associated with characteristically preserved specimens of the peculiar axes, only the epidermis and the central cylinder of which have not perished. Another rhizome-like axis of *Asteroxylon* is shown in transverse section in fig. 106, close to one of the peculiar axes, which is exceptional in having the cortex preserved. Isolated strands of xylem are present in

the clear peaty matrix. Adjoining the peculiar axis shown in fig. 103 the peat contains several more or less damaged specimens of sporangia still filled with the spores.

The rhizome or rhizome-like axes in this peat call for a brief reference. Some of them are most naturally regarded as rhizomes of *Asteroxylon*, but others have suggested a different interpretation. It is possible that we have in this block aerial axes of *Asteroxylon* with a simple strand of xylem that are difficult to differentiate from the rhizomes. It is unnecessary to multiply examples of such structures, the nature of which must be left doubtful, but it seems desirable to record our impression of the problem for future elucidation. It would be misleading to dismiss all these remains as rhizomes, which they undoubtedly closely resemble, without raising this question.

The association of the remains of *Asteroxylon* with the peculiar axes and sporangia is such as to suggest strongly the possibility of the latter constituting the fertile region of the same plant. We therefore describe them below, without giving them special names. It must, however, be clearly stated at the outset that we have not obtained evidence either of continuity or of histological identity which would convert the possibility or probability of their belonging to *Asteroxylon* into a certainty.

The peculiar axes and the sporangia will now be described as the possible sporangiophores and sporangia of *Asteroxylon*. Their reference to this plant will be discussed later in the paper.

(a) *The peculiar Axes or possible Sporangiohores of Asteroxylon.*

The general appearance of these in the peat is well shown in figs. 102 and 105 on Pl. XV. The preservation is poor, the cortical tissues having usually disappeared, but the outline is often traceable by the more or less persistent epidermis, and the stele also persists. In the stele the xylem, composed of narrow elements, is often still surrounded by remains of the collapsed thin-walled tissue, which, from its position, will be referred to as the phloem. The decay and disappearance of the cortex render the outline of the longitudinal sections of these axes difficult to follow, but it is evident that they were of considerable length, and branched dichotomously.

One of the specimens from the block in which they were first met with is shown in transverse section in fig. 107. The circular outline is only disturbed by contractions during preservation. The epidermis and cortex are poorly preserved. Centrally placed, there is a paired stele with two groups of xylem enclosed in a common investment of thin-walled phloem, which extends between them. The elements of both xylem and phloem are much narrower than in the undoubted vegetative organs of *Asteroxylon*.

The arrangement of the tissues in the steles of these axes exhibits a remarkable variety, which is best seen in comparing the transverse sections. Some characteristic examples are represented in figs. 108-116. In the simplest case the stele was single, and consisted of a solid core of xylem surrounded by a zone of phloem (figs. 108 ;

cf. 106, 118). There may be a small island of thin-walled phloem (fig. 109) or a larger island (fig. 110) within the strand of xylem. This internal phloem may be continuous with the outer phloem, making the cross section of the xylem horse-shoe shaped (fig. 111). Larger examples of this distribution of the tissues are also met with (fig. 114). Where the phloem extends right across, the two xylem strands are more or less distinctly and widely separate and embedded in a common mass of phloem (figs. 112, 113, 107). This leads on to two distinct steles lying within the same cortex (figs. 115, 116).

The range of structure in these specimens, though they cannot be regarded as constituting a series, is evidently consistent with a preparation for dichotomous division of the axis. The more or less completely double steles are, however, so frequent as compared with evidence of actual branching, that this may not be the complete explanation. The specimens so far described show no departing lateral traces.

Other examples have been met with, though less abundantly, in which the xylem of the stele was stellate or triangular in transverse section, and in which small traces were departing from the angles (figs. 117 and 119). These are more like small twigs of *Asteroxylon*, and it is noteworthy that in them the tracheides tend to be somewhat wider than is usual in these peculiar axes. This is well shown in fig. 119.

In yet other examples the stele was of the usual type for these axes, but was splitting off small lateral portions (figs. 120, 126 at *a*). It is of interest that these specimens were usually in the immediate neighbourhood of the sporangia, to be described below (fig. 126).

While the general relations of the tissues in these axes is satisfactorily ascertained, the poor preservation makes any detailed description of the tissues difficult. In only a few cases, such as the specimen illustrated in figs. 106 and 118, were all the tissues, including the cortex, fairly well preserved.

The epidermis is smooth, and its cells have their outer walls distinctly thickened and covered with a cuticle. As mentioned above, this layer often remains when the internal tissues have decayed (fig. 114). Stomata with short guard cells and a small pore have been observed in the epidermis (fig. 121). The cortex in the examples in which it is best preserved (fig. 118) is a uniform tissue composed of parenchymatous cells. Little can be said of the phloem except that it consisted of narrow, elongated, thin-walled elements. These, as preserved, tend to show in transverse section small dark triangular markings at the junction of the cells similar to those to which attention was directed in the corresponding tissue of *Hornea Lignieri*.

The tracheides composing the xylem were narrow, elongated tubes, with pointed ends and brown walls (fig. 122). Though they remain connected and show the outline clearly in transverse and longitudinal sections, repeated examination of numerous examples has failed to show the type of thickening of the tracheide walls. There was almost certainly a thickening that has been lost or altered by decay, but we are not prepared to place weight on such indications of its nature as we have yet observed.

In this respect, as well as in the narrow diameter of the tracheides, there is a remarkable difference from the xylem of undoubted portions of *Asteroxylon*. While, however, these differences are not to be under-estimated, it should be borne in mind that the diameter of the tracheides exhibits such a range in different specimens of these axes, and also in different axes of *Asteroxylon* in the same block of chert, that it is not easy to draw a dividing line on account of the size of the tracheides. This especially applies to some cylindrical strands of xylem, the tracheides of which, though narrow, show the thickening characteristic of *Asteroxylon* (cf. fig. 104).

(b) *Sporangia possibly belonging to Asteroxylon.*

The sporangia, which are associated with *Asteroxylon* and the axes just described in the block found by Dr GORDON, differ characteristically from those of the Rhyniaceæ. No confusion with the latter would be possible, and indeed no traces of *Rhynia* or *Hornea* occur in the peat of this block. The sporangia and spores in question have so far only been met with in this one specimen of the chert.

The spores and the remains of the sporangia occur throughout the block, but more abundantly in certain layers of it. The sporangia are more or less imperfect and decayed, and nothing can be said with certainty as to their connection with either the undoubted stems of *Asteroxylon* or with the peculiar axes that make up the peat. There is a suggestive association of them with some of the small axes, the stele of which is giving off branches (fig. 126), and the impression left by a study of the block is, that they were most probably borne on the peculiar axes, and that the latter were the sporangiophores of *Asteroxylon*.

In many cases only the thickened epidermal layer is preserved. This may be in fragments (fig. 124), or may give a fair idea of the general size and shape of the sporangium, and show that it dehisced at its wider free end (fig. 123). Here the epidermal cells are thickened on their inner and lateral walls, and in the immediate neighbourhood of the place of dehiscence they become shallower. The vertical section of the epidermal layer thus becomes pointed towards the line of dehiscence, as is particularly clearly seen in the two overlapping halves in fig. 125.

The specimen represented in fig. 126 gives some idea of the shape of the sporangium and its rather thick wall. It appears to have been pear-shaped, widening out from a thick stalk at the base, and about 1 mm. in length. There are some indications that a fairly thick zone of thin-walled tissue had been present within the epidermis and formed with this the sporangial wall.

Other specimens have the numerous spores still enclosed by the sporangial wall (fig. 103). The clearest example met with is represented in fig. 123. It is cut longitudinally, and shows the pear-shaped outline, with the epidermal layer becoming thickened in the upper portion as the place of dehiscence (X) is approached. There are remains of thin-walled tissue within the epidermis, and the cavity is filled with spores.

The mature spores are also found free in the peat. They are about  $64\mu$  in

diameter. The thin, smooth, cuticularised wall that alone persists has a characteristic bright yellow colour, and shows the tri-radiate marking. A number of spores lying free in a sporangium are shown in fig. 127. They have also been met with still grouped in tetrads.

THE CONNECTION OF THE PARTS DESCRIBED AND THE PROBABLE HABIT OF  
ASTEROXYLON.

Before we can attempt to compare *Asteroxylon* with other plants it is necessary to briefly summarise and discuss the connection of the various parts described in the preceding pages, and in the light of this to see what picture can be formed of the general habit of the plant. Our knowledge is unfortunately based on abundant fragments only, and we lack the assistance of impressions which would give in whole or in part the general form. The position of some of the parts and their mutual connection can, however, be deduced on conclusive evidence, while the picture can be extended with more or less probability to include other parts, the connection of which is not actually established.

The relation of the root-like branches of the rhizome to the peat, and the presence of stomata on the well-developed simple leaves, justify us in regarding *Asteroxylon* as a terrestrial plant which grew in and on the peaty soil.

It is also clear that the plant of *Asteroxylon* had a leafless, dichotomously branched, subterranean rhizome, some of the branches of which passed by a gradual transition into aerial leafy shoots. The transition is marked by the appearance first of small scale-leaves and then of the larger foliage leaves. The internal structure shows a corresponding change from the simple stele of the rhizome without leaf-traces to the stele of the stem with a stellate xylem giving off leaf-traces. Other branches of the rhizome of varying degrees of slenderness have been shown by their relations to the peat to have taken the place physiologically of a root-system. There is, however, no evidence to justify us in drawing a morphological distinction between roots and rhizomes.

The aerial shoots bore numerous, relatively small, simple leaves, each of which had a leaf-trace, though this did not extend into the free part of the leaf. The leaf-traces depart in more than one vertical series from each of the arms of the stellate xylem of the stem-stele. The aerial shoot must have formed a system of branches, maintaining a common plan of construction, but of successive degrees of slenderness. The branching in most cases observed has been lateral, but dichotomy is known to occur both in large stems and at the base of a lateral branch. The facts on the whole appear to indicate erect shoot-systems springing from the subterranean leafless rhizomes. We have met with nothing pointing to a horizontal leafy stem giving off erect branch systems on the one hand and rhizomes with their root-like branches on the other.

The above general mental picture of the vegetative organs of *Asteroxylon* may be said to be established in its main features. The connection of the various parts as belonging to one plant is proved by direct evidence of continuity and by the histological identity of important tissues.

On the other hand, conclusive evidence is wanting as to the fertile region and sporangia of *Asteroxylon*. On the ground of close association we regard it as probable that certain slender axes of peculiar structure and a type of dehiscent sporangia constituted the fertile region of this plant. Our knowledge of *Rhynia Gwynne-Vaughani*, *Rhynia major*, and *Hornea Lignieri* makes it certain that the structures in question have nothing to do with them; they either belong to *Asteroxylon* or to an additional plant from the bed, of the existence of which there is no further evidence. The weight we are prepared to lay on the peculiarly close association is indicated by not giving separate names to these peculiar axes and sporangia. It must be left for future investigation to confirm the assumed connection of these structures with *Asteroxylon*, or to show that they belong to another plant.

Even if our assumption is correct, we have no evidence as to the mode of connection of the peculiar fertile axes and sporangia with the vegetative shoots. The fertile axes might have replaced the leaves on a distal region of the shoot, or have been ultimate subdivisions of a fertile region continuing certain vegetative shoots.

If we assume that these parts were the fertile region of *Asteroxylon*, we can vaguely complete the picture of the plant, with the leafless rhizomes and branched leafy shoots, by fine branched leafless axes bearing dehiscent sporangia. The morphology and habit of the vegetative region of *Asteroxylon* are practically established by evidence. The suggestions as to the fertile region are, at most, probable.

#### DIAGNOSIS AND CLASSIFICATION.

*Asteroxylon*, Kidston and Lang, n.g.

*Diagnosis*.—Plant consisting of leafless rhizomes continuing into branched aerial stems bearing numerous small leaves. Stele of rhizome with a cylindrical strand of xylem, while the xylem of the stem-stele is stellate and gives off leaf-traces. The fertile region *probably* consisted of slender, branched, leafless axes bearing pear-shaped sporangia of moderate size, with definite dehiscence at the wider free end.

*Asteroxylon Mackiei*, Kidston and Lang, n.sp.

*Diagnosis*.—Rhizomes from over 5 mm. to under 1 mm. in diameter, some of the branches evidently behaving physiologically as roots; no absorbent hairs; epidermis, outer cortex and inner cortex; stele with zone of phloem around a central strand of xylem.

Transition region from rhizomes to shoots, with stomata in the epidermis and

small scale-leaves; stele, with the xylem within the zone of phloem becoming stellate and giving off leaf-traces; cortex as in the rhizomes.

Shoots from over 1 cm. to under 1 mm. in diameter, with simple leaves about 5 mm. long, without any vascular bundle in the free portion — the leaf-trace stopping at the leaf-base. Epidermis with thick outer walls and with stomata; narrow outer cortex; wide inner cortex usually differentiated into three zones, the middle zone having the vertical plates of tissue separated by wide intercellular spaces, and extending between the outer and middle zones as radial trabeculæ. Stele with stellate xylem without any mixture of parenchyma; protoxylem immersed in the ends of the rays; phloem between the rays and around the stele. Elements of phloem uniform, thin walled and elongated. Thickening of the tracheides, both of the protoxylem and metaxylem, spiral. Leaf-traces departing from the arms of the xylem in more than one vertical row; protoxylem surrounded by metaxylem, and this by a narrow zone of phloem. Trace ending in the outer cortex in the leaf-base. Branching lateral and dichotomous. Small stems of similar structure, but with xylem three-rayed, or even a cylindrical strand.

There is a *probability*, based on close association of the remains, that the fertile region of *Asteroxylon* consisted of slender, branched, leafless axes with peculiar structure and pear-shaped sporangia about 1 mm. long; sporangia with epidermal layer thickened towards the summit, where regular dehiscence took place. Homosporous. Spores developed in tetrads about  $64\mu$  in diameter.

*Locality*.—Muir of Rhynie, Aberdeenshire.

*Horizon*.—Old Red Sandstone, not younger than the Middle Division of the Old Red Sandstone of Scotland.

The Classification must remain to some extent obscure until the uncertainty as to the fertile region is cleared up. We suggest for the present associating *Asteroxylon* with *Psilophyton princeps* in a family of the Psilophytales to be called the Asteroxylaceæ.

The Classification of the Vascular Cryptogams or Pteridophyta associated together in the Rhynie bed of silicified peat would thus be as follows:—

## PTERIDOPHYTA.

### Class. PSILOPHYTALES.\*

#### Family. RHYNIACEÆ.

Genus. *Rhynia* (*R. Gwynne-Vaughani*, *R. major*).

*Hornea* (*H. Lignieri*).

#### Family. ASTEROXYLACEÆ.

Genus. *Asteroxylon* (*A. Mackiei*).

\* See Part I, *Trans. Roy. Soc., Edin.*, vol. li, p. 780, 1917.

## COMPARATIVE DISCUSSION.

The organisation of *Asteroxylon*, though more complex than that of *Rhynia* and *Hornea*, appears to be in some respects simpler than that of most Vascular Cryptogams. The uncertainty as to the fertile region of the plant makes full comparison difficult. On the other hand, there is the great advantage of a fairly complete knowledge of the anatomy of the vegetative organs of *Asteroxylon*.

On the grounds both of external organisation and of internal structure it is possible to make more or less close comparisons with some existing types of Pteridophyta and with some extinct archaic forms of this group. In the present imperfect, though growing, knowledge of the plants of Early Devonian times the recognition of points of comparison in various directions appears more desirable than attempts at a hypothetical completion of the facts. We propose in this discussion to confine speculation within definite limits, though it cannot be altogether avoided.

The position arrived at in the preceding section of this paper must be borne in mind in the following comparisons. The connection in one plant of the rhizomes, stems, and leaves of *Asteroxylon* is established on satisfactory evidence. That the small axes of peculiar structure and the sporangia constituted the fertile region of *Asteroxylon* is regarded as a probable presumption on the grounds of their close association with this plant and their absence in relation to the other vascular plants of the bed.

It should further be pointed out that, close as are some of the resemblances to be traced, *Asteroxylon* stands apart in certain respects from all other Vascular Cryptogams. One striking difference concerns the tracheides, those of the metaxylem as well as of the protoxylem having a peculiar type of spiral thickening. On account of this and other differences, and because of the imperfection of our knowledge of the plant as a whole, it is well to avoid drawing conclusions as to actual relationships.

## COMPARISONS.

It will be convenient to deal first with the undoubted vegetative organs of *Asteroxylon*, and then to extend the comparisons with other plants to the presumed fertile structures.

1. The organisation of the plant of *Asteroxylon* into leafless rhizomes and leafy aerial shoots finds a close parallel in the existing Psilotales. The absence of hairs even from the most root-like branches of the rhizome of *Asteroxylon* is a remarkable but minor point of difference. The resemblance holds even in points of detail as regards the absence of definite roots, the gradual passage of branches with the structure of the rhizome into aerial shoots, and the appearance of leaves, at first as small scales without leaf-traces, on the region of transition from the rhizome to the shoot. The comparison is not inconsistent with the very root-like behaviour of many of the branches of the rhizome of *Asteroxylon*. Something similar is shown,

though less strikingly, in the plants of *Psilotum* and *Tmesipteris*, and is brought out very clearly in the young stage of the latter. As HOLLOWAY'S\* account and figures show, one rhizome-like branch of the young plant on the prothallus turns up and becomes leafy, while the other extends into the soil in a root-like fashion. This second branch, however, in some cases becomes a leafy shoot.

The close comparison thus possible with *Psilotum* and *Tmesipteris* helps us in picturing the mode of growth of *Asteroxylon*, and adds weight to the view that the Psilotales have on the whole preserved a primitive type of organisation, and do not owe their simplicity to reduction.

In contrast to the comparison with the Psilotaceæ, that afforded by the species of *Lycopodium* and *Selaginella*, which show a distinction of subterranean rhizomes and aerial shoot-systems, is more superficial. The rhizomes in the Lycopodiaceæ bear small scale-leaves, and are probably to be regarded as modified aerial shoots. They also bear true roots.

2. As regards the external morphology of the leafy aerial shoots of *Asteroxylon* and the relations of stem and leaf, the comparison is perhaps closest to *Lycopodium* among existing plants, though it also holds in all essentials for the Psilotaceæ. The dichotomous and lateral branching also find parallels in the shoot-systems of the same plants.

In this connection the existence in Early Devonian times of a number of plants known as impressions, in which the stems were more or less closely clothed with small leaves, must be referred to here. A striking example is *Thursophyton* (*Lycopodites*) *Milleri*, from the Middle Old Red Sandstone of Scotland and Norway. This and other ancient plants, such as *Psilophyton* and *Arthrostroma*, will be considered further below.

3. In its anatomy *Asteroxylon* is most closely comparable with the Psilotaceæ and with *Lycopodium*, though some other plants must be mentioned.

The simple stele of the rhizome of *Asteroxylon* can be compared with that of the rhizome of *Psilotum* and *Tmesipteris*. There is a central strand of tracheides, without evident protoxylem, surrounded by phloem. The transition from this structure to the more complex stele of the leafy shoot also finds its closest parallel in the Psilotaceæ. As in these plants, it is associated with the appearance of small scale-leaves.

The stele of the aerial shoot of *Asteroxylon* corresponds in a striking fashion with that of the stem of *Lycopodium*. That there are also points of resemblance to the stele of *Psilotum* and to the primary structure of *Sphenophyllum* need only be mentioned in passing, since they concern features that are better shown in *Lycopodium*. Outstanding points of comparison between the steles of *Asteroxylon* and of some species of *Lycopodium* (e.g. *L. Selago*) are the circular outline of the stele as a whole, the stellate outline of the xylem with the ends of the rays often enlarged, the

\* HOLLOWAY, J. E., "The Prothallus and Young Plant of *Tmesipteris*," *Trans. N.Z. Institute*, vol. 1, 1917.

immersed or mesarch protoxylem\* in the ends of the rays, and the position of the phloem between and around the rays of the stellate xylem. The leaf-traces in both *Lycopodium* and *Asteroxylon* depart in more than one vertical series from each ray of the stellate xylem. They consist of a strand of xylem, with the smaller protoxylem elements in a central position, surrounded by a zone of soft tissue or phloem. The anatomical parallel between *Asteroxylon* and *Lycopodium* extends to the differentiation and zoning of the cortex, although the trabecular condition of the inner cortex is never so marked in the latter genus.

The termination of the leaf-trace in the leaf-base of *Asteroxylon*, so that the simple leaf-blade has no vascular bundle, is a noteworthy point of difference from *Lycopodium*. Other differences concern the type of thickening of the tracheides of the metaxylem, already referred to, and the absence of definitely specialised sieve-tubes in the phloem of *Asteroxylon*. In both these respects the stele of *Asteroxylon* appears to be less differentiated than that of *Lycopodium*.

A more distant comparison can be made between the stele of *Asteroxylon* with its stellate xylem and the stellate stem-steles of some Zygopterideæ, such as *Asterochlæna* and *Asteropteris*. The points of difference as regards both stele and leaf-traces are perhaps more important than those of agreement. The discovery in *Asteroxylon* of an ancient plant with a stele so like that of *Lycopodium* tends to strengthen the tentative comparisons that have been made between the Zygopteridean and *Lycopodium* steles.†

Another comparison that requires mention is that between the anatomy of *Asteroxylon* and *Stauropteris*. The vascular structure of the latter is clearly more fern-like. It would be dangerous to go further at present than to recognise that there are certain similarities in the arrangement of the tissues of the stele between *Stauropteris* and the stems of *Asteroxylon*. These features in the structure of *Stauropteris* have excited interest and proved a source of difficulty since the plant was first recognised.‡

4. The various comparisons made above were between the vegetative organs of *Asteroxylon* and other plants. The following comparisons concern the small axes with peculiar anatomy, and the associated sporangia which we regard as probably the fertile region of the same plant.

(a) The type of association of the plant remains in the block of chert which we owe to Dr GORDON is suggestively like the appearance presented by sections across the massed remains of *Stauropteris oldhamia*. It has been pointed out

\* The protoxylem of *Lycopodium* is usually exarch, as it may also be in *Asteroxylon*. Where larger leaf-traces join the stem-xylem in some species of *Lycopodium* a mesarch structure is shown. (Cf. SINNOTT, "On Mesarch Structure in *Lycopodium*," *Bot. Gazette*, 48, pl. x, fig. 5.)

† Cf. BERTRAND, P., *Progressus Rei Botanice*, Bd. iv, p. 276.

‡ The vascular structure of *Stauropteris* will evidently be regarded differently according to whether it is assumed that it is a specialised Zygopteridean frond (BERTRAND, P., *Études sur la Fronde des Zygopteridées*, Lille, 1909), or that it is a plant of more archaic type than the Zygopteridées, though tending in their direction (LIGNIER, *Bull. Soc. Bot. de France*, t. 59 (1912), p. 1).

that larger and smaller stems of *Asteroxylon*, leafless branches of simpler structure, and the peculiar axes and sporangia can be distinguished in this portion of the Rhynie peat (Pl. XV). The comparison is with the larger and smaller branches, the finer ultimate subdivisions, and the sporangia of *Stawropteris*. The reader may compare fig. 104 of this paper with fig. 321 of vol. ii of SEWARD'S *Fossil Plants*, or with fig. 1 on pl. i of BERTRAND'S memoir on the Zygoterideæ.

(b) No close comparisons can be made with certainty between the small axes with peculiar structure and other plants. The general resemblances they present, however, to ultimate fertile ramifications of *Stawropteris* on the one hand, and on the other to the sporangiophores of various extinct and existing Pteridophyta, may be indicated. We are inclined to attach considerable significance to this.

(c) The sporangia, with their thick wall, specially thickened epidermal layer without definite annulus, and terminal dehiscence, can be compared most closely with those of *Stawropteris*. Less close, but interesting, comparisons may be made with the sporangia of the Ophioglossaceæ, especially *Helminthostachys*, of the Psilotaceæ, and of *Lycopodium* and *Selaginella*.

5. Owing to the absence of conclusive evidence that the small axes with peculiar structure are the ultimate fertile branches of *Asteroxylon* and bore the associated sporangia, we enter a more speculative region in seeking for comparisons with the whole plant of *Asteroxylon* as completed by combining these as its reproductive organs.

If this assumption proves to be correct, the general habit and morphology of *Asteroxylon* would be comparable with that of some Early Devonian plants, the best known of which is *Psilophyton princeps*.

The plant of *Psilophyton princeps*, as reconstructed by DAWSON in his well-known figure,\* had horizontal rhizomes bearing more slender root-like appendages, erect branched aerial stems with small spine-like leaves, and large sporangia borne terminally on the smooth ultimate branches. The known specimens of the plant do not suffice to establish this reconstruction. There is doubt as to the appearance of the rhizome. The characters of the aerial stems, with their spiny leaves and dichotomous or lateral branching, are confirmed by specimens known from a number of localities. The actual connection of the smooth branched axes bearing the large sporangia with the leafy shoots is not established. They have, however, been found in association with the stems of *Psilophyton* in Norway and France as well as in the original locality at Gaspé in Canada, a circumstance that cannot be ignored. HALLE † has separated the stalked sporangia under the name *Dawsonites arcuatus*, on the ground of absence of proof of connection with *Psilophyton*. He, however, recognises in *Psilophyton Goldschmidti* a plant showing that smooth branch systems are borne

\* *Geological History of Plants*, fig. 19.

† HALLE, T. G., "Lower Devonian Plants from Røragen in Norway," *Kungl. Svenska Vetenskapsakademiens Handlingar*, Bd. 57 (1916), p. 1.

on main stems with small spine-like leaves. This, in our opinion, goes far to establish the organic connection of his *Dawsonites arcuatus* with *Psilophyton princeps*.

We are not in a position to enter into a critical consideration of the plant of *Psilophyton princeps* as a whole. In estimating the well-founded objections mentioned above to DAWSON'S reconstruction, it should be borne in mind that he had exceptional opportunities for considering the plant as preserved at Gaspé. Even if there is a considerable element of imagination in his reconstruction, it would appear that it represents with remarkable justice or prescience a particular type of plant characteristic of Early Devonian times.

The remains of *Asteroxylon* go far to establish the existence of another plant of Old Red Sandstone age showing all the regions of *Psilophyton* as reconstructed by DAWSON. The leafless rhizome with root-like branches, and the stems with small leaves and more or less lateral branching, are features of agreement dependent on definitely ascertained facts. So also are the smooth leafless axes with the sporangia, if these are rightly ascribed to *Asteroxylon*. The sporangia with terminal dehiscence, though of smaller size, have their counterpart in *Psilophyton*.

The two reconstructions, though both admittedly imperfect, exhibit a correspondence that makes them mutually supporting.

Some other Early Devonian plants may be considered in relation to the general type indicated by *Asteroxylon* and *Psilophyton*. Thus *Arthrostigma* agreed in the branched stems, with a central vascular strand, bearing pointed or spine-like leaves. Nothing is known of the subterranean parts of this plant, or of its reproductive organs. *Pseudosporochnus*, known from impressions in Bohemia, which are referred to the Middle Devonian, appears to have consisted of a stem-system of large size with continued subdivision of its branches. Some of the fine ultimate branches end in swellings, which are doubtfully referred to sporangia by POTONIE and BERNARD.\* There is no evidence of the existence of leaves in this plant, and the subterranean organs are unknown.

The crowded arrangement of the small leaves on the branched stems of *Thursrophyton (Lycopodites) Milleri*, from the Middle Devonian of Scotland and Norway, suggests comparison with *Asteroxylon*. Nothing is known of the reproductive organs of *Thursrophyton*. In this connection the prevalence of a number of types of land-plants of moderate size in the Middle Devonian flora of Norway, as described by NATHORST,† may be referred to. One of these, *Broggeria Norvegica*, seems worthy of consideration in relation to the possible fertile region of *Asteroxylon*. From NATHORST'S figures ‡ the plant may have had terminal fertile regions with crowded sporangiophores, and not a definite cone.

In another direction comparison may be extended to certain frond-like remains without any flattened lamina or pinnules (*Aphylopteris*, etc.) common in Middle

\* *Flore Devonienne de l'Étage H. de Burrande*, p. 32, figs. 71-72.

† NATHORST, "Zur Devonflora des westlichen Norwegens," *Bergens Museum Aarbok*, 1914-1915, No. 9.

‡ *Ibid.*, Taf. 3, figs. 5-7; Taf. 4, figs. 4-9.

Devonian rocks. Some specimens in which sporangia are terminal on ultimate ramifications are of special interest, and have been compared by other investigators to *Psilophyton*. These include *Dimeripteris*\* and *Rhacophyton condrusorum*† from the Upper Devonian. Perhaps the most striking comparison on these lines, however, is with the better, but still imperfectly, known plant *Stauropteris* from the Carboniferous rocks, especially if, as suggested by LIGNIER,‡ it should prove to have grown as an independent "frond," and not have been borne on a stem.

On reviewing the main comparisons, which we have been led to make or suggest with *Asteroxylon*, it will be seen that the only plants with which there may be agreement in total organisation are *Psilophyton* and some other more or less incompletely known archaic vascular plants. A definite conclusion cannot be reached on this question, owing to the uncertainty as to essential facts, both for *Asteroxylon* and all these other ancient plants.

The comparisons with the Psilotales as regards both general organisation and anatomy are close and striking. This group may be regarded as representing in a modified and specialised form the features of the *Asteroxylon* type of plant as persisting to the present time. The Psilotales must, however, be maintained as a distinct class of Pteridophyta.

The comparison with the Lycopodiales, and especially with *Lycopodium*, comes out clearly in the general habit, and particularly in the anatomy, though comparison cannot at present be extended to the reproductive organs. The antiquity of the general type of construction of the shoot and stele exhibited by *Lycopodium* is clearly established by our knowledge of *Asteroxylon*.

The characters of *Asteroxylon* suggest an advance from a more primitive type in the direction of the Lycopodiales rather than of the Filicales. There are, however, some interesting resemblances to archaic Ferns or plants which can be regarded as on the line to the Filicales.

The possible fertile region of *Asteroxylon*, though imperfectly known, appears to allow of comparison both with primitive Filicales and with the sporangiophore Pteridophyta. This suggests a general point of view from which all sporangiophores may be regarded.

#### THE CHARACTERS AND SYSTEMATIC POSITION OF ASTEROXYLON CONSIDERED IN RELATION TO LIGNIER'S VIEWS AS TO THE EVOLUTION OF PTERIDOPHYTA, AND HALLE'S APPLICATION OF THEM TO THE DEVONIAN FLORAS.

The characters of *Asteroxylon* and the comparisons with other Pteridophyta suggested above are consistent with a general view of the sporophyte in land-plants

\* SCHMALHAUSEN, J., "Ueber devonische Pflanzen aus dem Donetz-Becken," *Mém. du Comité Géol.*, vol. viii, No. 3, p. 29, 1894.

† CRÉPIN, F., "Description de quelques plantes fossiles de l'étage des Psammites du Condroz (Dévonien Supérieur)," *Bull. de l'Acad. roy. de Belgique*, vol. xxxviii, p. 1, 1874. (*Psilophyton condrusorum*.) CRÉPIN, F., "Observations sur quelques plantes fossiles de dépôts dévonien, etc.," *Bull. Soc. roy. de Bot. de Belgique*, vol. xiv, p. 224, 1875. (Footnote, *Rhacophyton condrusorum*.)

‡ *Loc. cit.*, 1912.

that has emerged and been further developed of late years. On this view the plant of the Vascular Cryptogams is comparable with, and derived from, a thalloid plant-body such as we meet with in a number of the higher Algae. In its modern form it was first developed by POTONIÉ, but it is especially in the form it assumed in the speculations of LIGNIER that it applies to Early Devonian plants. This investigator indeed made special use of DAWSON'S reconstruction of *Psilophyton* in formulating his theory.

It will avoid unnecessary repetition if we give a free summary of those salient features of the theoretical views of the late Professor LIGNIER, and of the discussion of them in relation to the Devonian flora by Dr HALLE, which appear to us to bear on the consideration of *Asteroxylon*. The reader is referred to the full statements of the views of these investigators as given in the literature cited below.\*

The primitive type of plant-body in the Pteridophyta is supposed by LIGNIER to have consisted of erect, dichotomously branched, cylindrical cauloids bearing small flattened phylloids and with terminal sporangia. The later origin of roots is supposed to have taken place by the transformation of certain subterranean cauloids. *Psilophyton* is instanced as exhibiting most clearly this primitive type. Among existing plants the Psilotales are regarded as differing chiefly in the localisation of the sporangia on reduced branches. From such a primitive type of plant-body the Lycopods are derived by further specialisation, their leaves being regarded as phylloids. The leaves of the Filicales, on the other hand, are of a different origin, being derived by the specialisation of certain cauloidal branch-systems. In the more primitive forms (*Dimeripteris*, *Stauropteris*) the bi-valvular sporangia were borne terminally on the ends of cauloids, as they were in *Psilophyton*. The flattened leaf-blades arose later by agglomeration of the cauloids into pinnules, and the sporangia, at first marginal, then became situated on the lower surface.

LIGNIER'S view is susceptible of further simplification by TANSLEY'S suggestion † that the leaves of the Lycopodiales may have been derived by "foliar specialisation of short undivided branchlets of the thallus, instead of whole branch-systems as in the Filicinean type." This does away with the sharp distinction of phylloids and cauloids.

The general view provides us with a conception of a common origin of the divergent types of sporophyte represented by the Psilotales, Lycopodiales, and Filicales. ‡

\* LIGNIER, M. O., "Equisétales et Sphénohyllales: Leur origine filicinéenne commune," *Bull. Soc. Linn. Normandise*, sér. 5, vol. 7, 1903, p. 93. "Essai sur l'Évolution Morphologique du règne végétal," *Comptes de l'Assoc. Française pour l'Avancement des Sciences*, 1908, p. 580. "Le Stauropteris Oldhamia Binney et les Coenoptéridées à la lumière de la théorie du mériphyte," *Bull. Soc. Bot. de France*, t. 59, 1912, p. 1.

HALLE, T. G., "Lower Devonian Plants from Røragen in Norway," *Kungl. Svenska Vetenskapsakad. Handlingar*, Bd. 57, p. 1.

† *Lectures on the Evolution of the Filicinean Vascular System*, p. 9. (Reprint, 1908.)

‡ For the present purpose it is unnecessary to complicate the discussion by entering into the consideration of the Equisétales and Sphenophyllales.

In a recent paper HALLE has discussed the Early Devonian flora on these lines. He surveys the assemblages of plants described from various localities, and indicates the general distinction between those of Lower and Middle Devonian strata, and the contrast of both with the plants of the Upper Devonian. In his general botanical conclusions he points out the prevalence of plants with relatively small spine-like leaves (*Arthrostroma*, *Psilophyton*) in the Lower Devonian, and suggests that from such plants we can pass to the undoubted Lycopodiaceous forms of the Upper Devonian. He also points out the prevalence in the Lower Devonian of remains like the branched rachises of fern-fronds, but with no indication of pinnules or laminae. He suggests that the points of comparison of these, on the one hand with such a form as *Psilophyton Goldschmidti*, and on the other with fern-fronds, enables us to think of the Lycopsidea and Pteropsida as connected in origin from a common form that was already vascular. HALLE regards the fructification of *Psilophyton* as described by DAWSON (which, however, he separates under the name of *Dawsonites arcuatus*) as the best evidence of the beginning of the Filicinean phylum in the Older Devonian flora. He points out the prevalence in succeeding ancient Palæozoic strata of large sporangia borne on special branched fronds without a lamina. The natural interpretation is that these fertile fronds represent the primitive state, and that the flattened pinnules are a later development by cladodification as suggested by LIGNIER, the sporangia being pre-existent in respect to the laminae of the pinnules.

We have summarised the views of LIGNIER instead of discussing the question afresh, because, without accepting his theory in all details, we find ourselves in general agreement with his conception of a divergent progression from the primitive land-plants towards the more specialised Lycopodiales on the one hand and towards the Filicinean type of plant on the other. HALLE'S survey of the Devonian floras in the light of these views also appears to us to be a fair statement of the present bearing of the imperfectly known facts. It seems advisable to keep the general conception on broad lines, in the hope that as our knowledge of the historical data increases the details will emerge naturally. The interest and significance of the more generalised plants, the external form and internal structure of which are becoming better known, will remain even if it should prove that higher types coexisted with them.

The characters of *Asteroxylon* are consistent with, and support, the conception of the general course of the differentiation of early land-plants outlined above. *Asteroxylon* appears to agree with *Psilophyton* in possessing in a generalised and archaic form characters that are definitely specialised in the Psilotales, Lycopodiales, and Filicales. The Geological age and succession of the Early Devonian plants are on the whole consistent with the origin of the various groups of Vascular Cryptogams from a common source. If we think of *Psilophyton* as giving a fair idea of the characters of this type, *Asteroxylon* shows indications of divergence in the direction

of the Lycopods, while the characters of *Stauropteris* (though this plant is in its own way more advanced and specialised) may suggest the connection of the fern type.

Partly because of the insufficiency of our knowledge of the plants, and partly because of the divergent tendencies towards more specialised groups which they exhibit, it must be a matter of difficulty to define the characters of the group to which *Asteroxylon* and *Psilophyton* belong. We have reason for regarding these plants as differentiated into rhizomes, branched aerial shoot-systems with relatively small leaves, and leafless branches bearing dehiscent sporangia. Such plants have a more complex organisation than the Rhyniaceæ, with which they will be compared below. The present state of our knowledge regarding them would appear to be fairly, though tentatively, expressed by distinguishing a more complex family of the Psilophytales, which may be termed the Asteroxylaceæ.

#### COMPARISON OF ASTEROXYLON WITH THE RHYNIACEÆ. CONCLUSION.

*Asteroxylon* must, in conclusion, be compared with the still simpler type of Vascular Cryptogams represented by the Rhyniaceæ.

The simple structure of the rhizome and basal region of the plant in *Asteroxylon* is clearly comparable with that found throughout the plants of the Rhyniaceæ. There are also indications of a similarly simple construction in some ultimate distal divisions of *Asteroxylon*. In the leafy middle region of the shoot of *Asteroxylon* a complication in internal structure accompanies that in the external form.

The small dehiscent sporangia which are presumed to belong to *Asteroxylon* appear to be of an advanced and specialised type as compared with those of *Rhynia* and *Hornea*.

*Asteroxylon* differs from *Rhynia* and *Hornea* in the presence of undoubted leaves on the aerial stems. The only structures in the Rhyniaceæ which suggest a comparison with leaves are the peculiar hemispherical projections on the stems of *Rhynia Gwynne-Vaughani*, and it is possible to regard these as affording a clue to the leaves of *Asteroxylon*. On the other hand, we are acquainted in the Algæ with a number of independent examples of the integration of originally similar members of a thalloid branch system into a new whole in which the continued axis of growth appears as a relatively main "stem" bearing the subordinated branches or "leaves"; the relation of the shoot in *Asteroxylon* to the thalloid type of plant-body in the Rhyniaceæ may alternatively be regarded in some such fashion.

To enter more fully into the meaning of the differences between the organisation of *Asteroxylon* and that of the Rhyniaceæ would involve a discussion of the nature of the leafy shoot. We shall not enter upon the consideration of the general question here.

The Vascular Plants which grew together in the Rhynie peat have fortunately preserved for us the structure of examples of both the simple and the more complex types of the archaic plants which we associate as the Psilophytales. They do not

demonstrate the passage of the one type to the other, and perhaps a record of this was hardly to be looked for.

In *Rhynia* and *Hornea* we have revealed to us a much simpler type of Vascular Cryptogam than any with which we were previously acquainted. This type suggests the convergence of Pteridophyta and Bryophyta backwards to an Algal stock.

The knowledge of *Asteroxylon* confirms and enriches our conception of a more complex but archaic type of the Vascular Cryptogams which supports the idea of the divergence of the great classes of Pteridophyta from a common type, and links this on to the simpler Rhyniaceæ.

## EXPLANATION OF PLATES.

(All the figures are from untouched photographs.)

*Asteroxylon Mackiei*, Kidston and Lang.

## PLATE I.

Fig. 1. General view of a vertical section from the upper part of bed A' 1. Large stems of *Asteroxylon* are enclosed in the dark sandy matrix above. The clear peat below is composed of *Hornea*, but contains rhizomes of *Asteroxylon*.  $\times 2\frac{2}{3}$ . (No. 2461.)

Fig. 2. Similar section from another block of the silicified peat from the same bed. In the sandy matrix above are stems of *Asteroxylon*, and at (a) a large rhizome containing a smaller intrusive one. Into the peat below, made up of *Hornea* and *Rhynia major*, rhizomes of *Asteroxylon* extend vertically; the one at (b) perforates a rhizome of *Hornea*.  $\times 2$ . (No. 2462.)

Fig. 3. Small rhizomes in relation to large stems of *Asteroxylon* enclosed in the sandy matrix. a, rhizome cut transversely in the cortex of the large stem; b, rhizome cut longitudinally as it lay in the peat and passed through another stem of *Asteroxylon*.  $\times 14$ . (No. 2463.)

Fig. 4. Large rhizome in transverse section into which another rhizome of considerable size has intruded, while the cortex of this in turn encloses two small rhizomes. o.c., outer cortex of the large rhizome; i.c., inner cortex; ph., phloem; x., xylem.  $\times 14$ . (No. 2464.)

Fig. 5. Transverse section of rhizome of moderate size showing division of stele preparatory to dichotomous branching.  $\times 14$ . (No. 2465.)

Fig. 6. Slightly oblique longitudinal section of a rhizome of moderate size. ep., epidermis; o.c., outer cortex; i.c., inner cortex; ph., phloem; x., xylem.  $\times 14$ . (No. 2466.)

Fig. 7. Partially decayed specimen of rhizome in obliquely longitudinal section showing dichotomous branching.  $\times 14$ . (No. 2467.)

## PLATE II.

Fig. 8. Portion of the small rhizome in longitudinal section shown in fig. 3.  $\times 33$ . (No. 2463.)

Fig. 9. The small rhizome in transverse section shown in fig. 3.  $\times 33$ . (No. 2463.)

Fig. 10. Portion of the xylem of the small rhizome in figs. 3 and 8 showing the spirally thickened tracheides.  $\times 210$ . (No. 2463.)

Fig. 11. Portion of the xylem of the rhizome in fig. 6. The imperfectly preserved phloem is seen to the right.  $\times 210$ . (No. 2466.)

Fig. 12. Portion of a longitudinal section of the large rhizome in fig. 6 showing the superficial tissues well preserved. ep., epidermis; o.c., outer cortex; i.c., inner cortex.  $\times 105$ . (No. 2466.)

Fig. 13. Portion of the outer tissues of another large rhizome in longitudinal section. ep., epidermis; o.c., outer cortex; i.c., inner cortex.  $\times 60$ . (No. 2468.)

Fig. 14. Two small root-like rhizomes in transverse section.  $\times 33$ . (No. 2469.)

Fig. 15. Portion of clear peat, including above an obliquely longitudinal section of a rhizome of moderate size, and below a transverse section of the transition region to the shoot. The latter, on the left, has a well-preserved epidermis, and bears small scale-leaves. A small intrusive root-like rhizome is enclosed in its cortex below.  $\times 14$ . (No. 2470.)

Fig. 16. Longitudinal section of an axis with indications of small scale-leaves (*sc. l.*) and of leaf-traces (*l. t.*), but with structure closely similar to that of a large rhizome. *ep.*, epidermis; *o. c.*, outer cortex; *i. c.*, inner cortex; *ph.*, phloem; *x.*, xylem.  $\times 14$ . (No. 2439.)

## PLATE III.

Fig. 17. Transverse section of an axis of the transition region showing hardly any advance on the structure of the rhizome. The stele has given off a smaller branch.  $\times 14$ . (No. 2469.)

Fig. 18. Transverse section of a more advanced phase of the transition from the rhizome to the leafy shoot. Small scale-leaves are borne on the surface, and the xylem is angled but not giving off leaf-traces.  $\times 14$ . (No. 2471.)

Fig. 19. Transverse section of a specimen of the transition region bearing small scale-leaves. Two steles are enclosed in the common cortex, preliminary to branching. The xylem is stellate and giving off leaf-traces.  $\times 14$ . (No. 2456.)

Fig. 20. Transverse section from the same axis as fig. 17, showing all the tissues of the early transition region. *ep.*, epidermis; *o. c.*, outer cortex; *i. c.*, inner cortex permeated with fungus; *ph.*, phloem; *x.*, xylem.  $\times 33$ . (No. 2472.)

Fig. 21. Portion of fig. 19 more highly magnified, showing the stellate xylem (*x.*), the distribution of the well-preserved phloem (*ph.*), and a leaf-trace (*l. t.*) in the cortex, with xylem surrounded by phloem.  $\times 33$ . (No. 2456.)

Fig. 22. Portion of fig. 16 more highly magnified. *ep.*, epidermis; *o. c.*, outer cortex; *i. c.*, inner cortex with fungus; *ph.*, phloem; *x.*, xylem.  $\times 33$ . (No. 2439.)

Fig. 23. Scale-leaf from the transition region.  $\times 60$ . (No. 2473.)

Fig. 24. Transverse section of an advanced stage in the transition region, with small scale-leaves and simple cortex, but with a stele like that of the larger leafy shoots.  $\times 14$ . (No. 2473.)

## PLATE IV.

Fig. 25. Transverse section of two axes, separating in branching, with the structure of an early stage of the transition region. Above is another more advanced example, the quadrangular xylem of which is giving off leaf-traces.  $\times 14$ . (No. 2474.)

Fig. 26. Transverse section of small root-like rhizome. *o. c.*, outer cortex; *i. c.*, inner cortex; *ph.*, phloem; *x.*, xylem.  $\times 60$ . (No. 2475.)

Fig. 27. Transverse section of another small root-like rhizome with the epidermis (*ep.*) preserved.  $\times 60$ . (No. 2476.)

Fig. 28. Portion of clear peat showing two transverse sections of small rhizomes. The one on the left shows the epidermis well preserved on one side.  $\times 33$ . (No. 2477.)

Fig. 29. Transverse section of small rhizome. *o. c.*, outer cortex; *i. c.*, inner cortex; *ph.*, phloem; *x.*, xylem.  $\times 60$ . (No. 2476.)

Fig. 30. Transverse section of small leafy shoot.  $\times 14$ . (No. 2479.)

Fig. 31. Longitudinal section of a large leafy shoot showing two leaves attached to the stem. The dark bodies in the inner cortex are fungi.  $\times 14$ . (No. 2476.)

## PLATE V.

Fig. 32. Tangential section of leafy shoot showing two leaves in longitudinal section, that on the left attached to the stem.  $\times 14$ . (No. 2471.)

Fig. 33. Transverse section of medium-sized stem showing the leaves as they separate from the leaf-bases.  $\times 20$ . (No. 2480.)

Figs. 34, 35. Two successive tangential sections of a shoot showing the termination of a leaf-trace in the leaf-base, the attachment of the leaf and its free portion.  $\times 14$ . (Fig. 34, No. 2481; Fig. 35, No. 2482.)

Fig. 36. Transverse section of one-half of a bud-like grouping of leaves, the other half being lost by the brecciation of the chert.  $\times 33$ . (No. 2483.)

Fig. 37. Free portions of a number of well-preserved leaves in transverse section.  $\times 33$ . (No. 2484.)

Fig. 38. Complete leaf in longitudinal section.  $\times 20$ . (No. 2456.)

Fig. 39. Portion of the leaf in fig. 38 showing the papillate epidermal cells.  $\times 60$ . (No. 2456.)

Fig. 40. Longitudinal view of a number of leaves in a section of the chert, showing stomata (*st.*) in surface view.  $\times 105$ . (No. 2465.)

## PLATE VI.

Fig. 41. Transverse section of large stem. *o.c.*, outer cortex; *i.c.o.*, outer zone of inner cortex; *i.c.m.*, middle (trabecular) zone of inner cortex; *i.c.i.*, inner zone of inner cortex; *ph.*, decayed phloem; *x.*, xylem.  $\times 14$ . (No. 2464.)

Fig. 42. Transverse section of stem, in which the outer cortex and the leaf-bases are prominent owing to the dark cell contents.  $\times 14$ . (No. 2485.)

Fig. 43. Transverse section of stem. *o.c.*, outer cortex; *i.c.m.*, trabecular middle zone of inner cortex; *i.c.i.*, inner zone of inner cortex; *ph.*, decayed phloem; *x.*, xylem; *lt.*, leaf-traces in the neighbourhood of the stele and in the outer cortex.  $\times 14$ . (No. 2490.)

Fig. 44. Transverse section of a moderate-sized stem showing the corresponding arrangement of tissues.  $\times 14$ . (No. 2491.)

Fig. 45. Transverse section of moderate sized stem with more massive stellate xylem than that in the preceding figure. *o.c.*, outer cortex; *i.c.o.*, outer zone of inner cortex; *i.c.m.*, middle trabecular zone of inner cortex; *i.c.i.*, inner zone of inner cortex.  $\times 14$ . (No. 2492.)

Fig. 46. Transverse section of small stem; leaves in transverse section occur in the peat around.  $\times 14$ . (No. 2468.)

Fig. 47. Transverse section of small stem with well-marked trabecular zone of the inner cortex and three-rayed xylem. In the peat, on the right, are small twigs with imperfectly-preserved cortex, giving the appearance of dichotomous branching and of a cylindrical strand of xylem.  $\times 14$ . (No. 2493.)

Fig. 48. Group of small twigs with imperfectly preserved cortex in transverse section.  $\times 14$ . (No. 2466.)

## PLATE VII.

Fig. 49. Obliquely transverse section of a stem with distinct outer cortex (*o.c.*) and uniform inner cortex (*i.c.*). Large traces, one apparently for a branch and the other for a leaf, are departing from the stele.  $\times 14$ . (No. 2486.)

Fig. 50. Transverse section of the stele of the stem shown in fig. 47. *ph.*, well-preserved phloem; *x.*, xylem.  $\times 60$ . (No. 2493.)

Fig. 51. Transverse section of stele in which the phloem extends right across, separating the xylem into distinct groups.  $\times 60$ . (No. 2487.)

Fig. 52. Transverse section of stele in which the imperfection of the central region of the xylem has led to the partial separation of the numerous enlarged ends of the rays.  $\times 33$ . (No. 2472.)

Fig. 53. Transverse section of stele with massive four-rayed xylem (*x.*) and partially-preserved phloem (*ph.*). *lt.*, leaf-traces.  $\times 33$ . (No. 2488.)

Fig. 54. Transverse sections of two small stems with the well-preserved xylem giving off leaf-traces enclosed by the cortex in which all trace of the tissues has disappeared.  $\times 20$ . (No. 2449.)

Fig. 55. Transverse section of xylem with leaf-traces departing from the enlarged ends of the rays.  $\times 33$ . (No. 2462.)

Fig. 56. Transverse section of xylem showing the position of the groups of immersed protoxylem and the arrangement of the departing leaf-traces.  $\times 33$ . (No. 2489.)\*

Fig. 57. Transverse section of the stele of the stem in fig. 44 showing the departure and arrangement of the small leaf-traces.  $\times 60$ . (No. 2491.)

\* In this and the preceding figure the soft tissues have been lost in the photograph in bringing out the details of the xylem.

## PLATE VIII.

Fig. 58. Transverse section of small shoot with the differentiation of tissues uncompleted. *l.*, leaf; *o.c.*, outer cortex; *i.c.m.*, middle layer of inner cortex; *i.c.i.*, inner layer of inner cortex; *s.*, undifferentiated stele.  $\times 60$ . (No. 2486.)

Fig. 59. Transverse section of stem in a region behind the apex where the differentiation of the stelar tissues has just begun.  $\times 10$ . (No. 2454.)

Fig. 60. Transverse section of the stele of the section below that shown in fig. 59. The poles of the developing stem-xylem are marked *x*; the other dark groups of elements are leaf-traces.  $\times 60$ . (No. 2473.)

Fig. 61. Epidermis of two adjacent stems showing the thick outer wall and cuticle.  $\times 105$ . (No. 2486.)

Fig. 62. Epidermis (*ep.*) and outer cortex (*o.c.*) from the transverse section of a small stem.  $\times 105$ . (No. 2486.)

Fig. 63. Longitudinal section of stem. *o.c.*, outer cortex; *i.c.o.*, outer zone of inner cortex; *i.c.m.*, middle (trabecular) zone of inner cortex; *i.c.i.*, inner zone of inner cortex; *x*, xylem.  $\times 14$ . (No. 2494.)

Fig. 64. Oblique section of stem showing the complete course of a leaf-trace (*l.t.*) from the neighbourhood of the stele to a leaf-base.  $\times 14$ . (No. 2495.)

Fig. 65. Stoma in surface view and adjoining epidermal cells with contracted dark contents.  $\times 210$ . (No. 2491.)

Fig. 66. Stoma in vertical section across the pore.  $\times 210$ . (No. 2496.)

## PLATE IX.

Fig. 67. The inner cortex in transverse section showing the middle (trabecular) zone well preserved. *i.c.o.*, outer zone; *i.c.m.*, middle zone; *i.c.i.*, inner zone.  $\times 33$ . (No. 2475.)

Fig. 68. Well-preserved inner zone of the inner cortex (*i.c.i.*). *i.c.m.*, middle (trabecular) zone.  $\times 33$ . (No. 2497.)

Fig. 69. Transverse section of stele showing distinct layer of cells (*en.*) in the position of an endodermis.  $\times 33$ . (No. 2506.)

Fig. 70. Longitudinal section of partially-preserved phloem (*ph.*) of stem. *x*, xylem; *i.c.i.*, inner zone of inner cortex.  $\times 60$ . (No. 2498.)

Fig. 71. Portion of middle zone of inner cortex not clearly trabecular but showing the cells and the intercellular spaces well.  $\times 105$ . (No. 2497.)

Fig. 72. Transverse section of stele of stem with exceptionally well-preserved phloem (*ph.*). *x*, xylem; *i.c.i.*, inner zone of inner cortex.  $\times 33$ . (No. 2475.)

Fig. 73. Portion of the epidermis of stem in the transition region in surface view showing stomata with large pores.  $\times 210$ . (No. 2471.)

## PLATE X.

Figs. 74-76. Ends of the rays of stellate xylem from the same stele in transverse section showing the structure of the tracheides. *px.*, groups of small elements of the protoxylem.  $\times 105$ . (No. 2499.)

Figs. 77-79. Longitudinal sections of the xylem of the stem showing the structure of the tracheides. *px.*, narrow elements of protoxylem.  $\times 210$ . (Fig. 77, No. 2500; Figs. 78, 79, No. 2492.)

Fig. 80. Large leaf-trace in transverse section showing the central protoxylem.  $\times 210$ . (No. 2500.)

Fig. 81. Similar leaf-trace beside an arm of the stem xylem with its immersed protoxylem.  $\times 210$ . (No. 2501.)

Fig. 82. Small leaf-trace separating from an arm of the xylem in which the protoxylem is less evident.  $\times 210$ . (No. 2501.)

## PLATE XI.

Fig. 83. Transverse section of stele from same stem as fig. 51 showing a branch-trace (*br. tr.*) preparing to separate from one ray of the xylem.  $\times 33$ . (No. 2483.)

Fig. 84. Transverse section of stem with a branch-trace (*br. tr.*) on its way out through the cortex.  $\times 14$ . (No. 2502.)

Fig. 85. Transverse section of large stem with a branch-trace (*br. tr.*) just emerging from the cortex.  $\times 14$ . (No. 2459.)

Fig. 86. Next section of the same showing the branch (*B*) still connected with the stem.  $\times 14$ . (No. 2461.)

Fig. 87. Next section of the small branch, the xylem of which has now become typically stellate.  $\times 14$ . (No. 2492.)

Fig. 88. Transverse section of stem showing a small branch (*B*) connected to it by a narrow web of cortex.  $\times 14$ . (No. 2503.)

Fig. 89. Transverse section showing two steles (*a* and *b*) with imperfectly stellate xylem, enclosed in the same cortex.  $\times 14$ . (No. 2459.)

## PLATE XII.

Fig. 90. Transverse section of stem surrounded by the free portions of leaves and bearing a small leafy, lateral branch cut longitudinally.  $\times 14$ . (No. 2478.)

Fig. 91. Stem cut transversely and departing branch (*B*) cut longitudinally.  $\times 7\frac{1}{2}$ . (No. 2470.)

Fig. 92. Further portion of the branch in fig. 91 showing the stele and leaf-traces.  $\times 20$ . (No. 2470.)

Fig. 93. Tangential longitudinal section of the cortex of a stem showing in continuity with it a branch in transverse section with a stele like that of the larger rhizomes. *ph.*, phloem of branch; *x.*, xylem of branch.  $\times 14$ . (No. 2470.)

Fig. 94. Transverse section of branch-stele in the cortex of a stem. The strand of xylem is surrounded by the collapsed phloem.  $\times 33$ . (No. 2504.)

## PLATE XIII.

Fig. 95. Stem with the structure of the advanced transition region with a small lateral branch still attached.  $\times 12$ . (No. 2477.)

Fig. 96. Large stem of typical structure surrounded by transverse sections of leaves. The stellate xylem of the stele is double as if in preparation for dichotomous branching.  $\times 14$ . (No. 2479.)

## PLATE XIV.

Fig. 97. Transverse section of a stem showing the preparation for the departure of a branch-trace (*br. tr.*) from one arm of the stellate xylem.  $\times 7\frac{1}{2}$ . (No. 2505.)

Fig. 98. Transverse section of the same stem at a higher level. The branch-trace (*br. tr.*) has increased in size where it lies in the neighbourhood of the parent stele. Adjacent to the main stem, but not in connection with it, the branch is cut where it is dividing into two (*Ba, Bb*).  $\times 7\frac{1}{2}$ . (No. 2506.)

Fig. 99. Transverse section of the same stem at a still higher level. The stele of the branch (*br. tr.*) is cut on its way out through the cortex of the main stem, and two steles (*Ba, Bb*) are contained in the cortex of the further portion of the branch, which is bent back.  $\times 7\frac{1}{2}$ . (No. 2507.)

Fig. 100. The stem in fig. 98 more highly magnified. *c.*, cortex of main stem; *en.*, layer in position of an endodermis limiting the stele of the main stem; *c. br.*, cortex of branch; *X*, discontinuity between the cortical tissues of the emerging branch and of the main stem.  $\times 14$ . (No. 2506.)

Fig. 101. Region of discontinuity between the cortex of the main stem and of the branch in fig. 100 more highly magnified. *c.*, cortex of main stem; *c. br.*, cortex of branch.  $\times 33$ . (No. 2506.)

## PLATE XV.

Fig. 102. Portion of a section of the silicified peat of the block found by Dr GORDON. A large stem of *Asterozylon* is seen above, below there are smaller stems, while the track of a rhizome is traceable across the peat formed of the small peculiar axes.  $\times 14$ . (No. 2505.)

Fig. 103. Another portion showing sporangia filled with spores (*s. s.*) in the neighbourhood of one of the peculiar axes with two steles.  $\times 30$ . (No. 2508.)

Fig. 104. Another portion showing a large stem of *Asteroxylon* (*a*), two cylindrical strands of xylem (*b*) composed of *Asteroxylon* tracheides, fragments of xylem of *Asteroxylon* (*c*), and a peculiar axis with its cylindrical strand of xylem (*d*).  $\times 105$ . (No. 2509.)

Fig. 105. Another portion showing a rhizome-like structure which is cut transversely and is giving off a small lateral branch, embedded in the peat formed of characteristic specimens of the peculiar axes.  $\times 33$ . (No. 2509.)

Fig. 106. Another portion showing a rhizome-like axis of *Asteroxylon* at *a*, and at *b* one of the peculiar axes with the cortex preserved. These are embedded in a peat formed of fragments of *Asteroxylon*.  $\times 33$ . (No. 2510.)

## PLATE XVI.

Fig. 107. Transverse section of one of the small peculiar axes. *ep.*, epidermis; *c.*, cortex; *ph.*, phloem; *x. x.*, two strands of xylem.  $\times 33$ . (No. 2511.)

Figs. 108-113. Steles of the peculiar axis in transverse section showing different distribution of the xylem and phloem. Description in the text (p. 660).  $\times 60$ . (Fig. 108, No. 2508; Fig. 109, No. 2507; Fig. 110, No. 2505; Fig. 111, No. 2507; Fig. 112, 2509; Fig. 113, No. 2507.)

Fig. 114. Stele of peculiar axis showing horse-shoe shaped xylem (*x.*) and its relation to the phloem (*ph.*).  $\times 60$ . (No. 2512.)

Figs. 115, 116. Specimens of the peculiar axis with two distinct steles enclosed in the one epidermis. The cortex, as usual, has decayed.  $\times 60$ . (Fig. 115, No. 2505; Fig. 116, No. 2506.)

Fig. 117. Specimen of the peculiar axis with small traces departing from the stele.  $\times 33$ . (No. 2507.)

Fig. 118. Portion of the peculiar axis with the cortical tissues preserved shown in fig. 106. *ep.*, epidermis; *c.*, cortex; *x.*, xylem.  $\times 105$ . (No. 2510.)

## PLATE XVII.

Fig. 119. Transverse section of a specimen of the peculiar axis the xylem of which consists of larger tracheides than usual and is giving off traces radially.  $\times 60$ . (No. 2506.)

Fig. 120. Specimens of the peculiar axis the steles of which are giving off smaller portions laterally. There are fragments of the sporangial walls in the adjacent matrix.  $\times 60$ . (No. 2509.)

Fig. 121. Stoma in surface view from the epidermis of one of the peculiar axes.  $\times 160$ . (No. 2505.)

Fig. 122. Xylem of one of the peculiar axes in longitudinal section showing the narrow tracheides without recognisable thickening.  $\times 105$ . (No. 2512.)

Fig. 123. Longitudinal section of a sporangium filled with spores. X, the place of dehiscence in the thickened epidermis.  $\times 50$ . (No. 2513.)

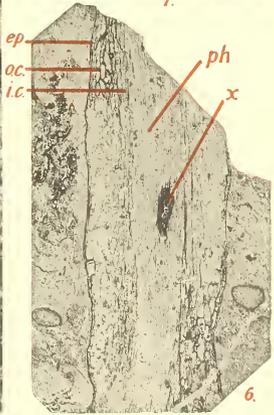
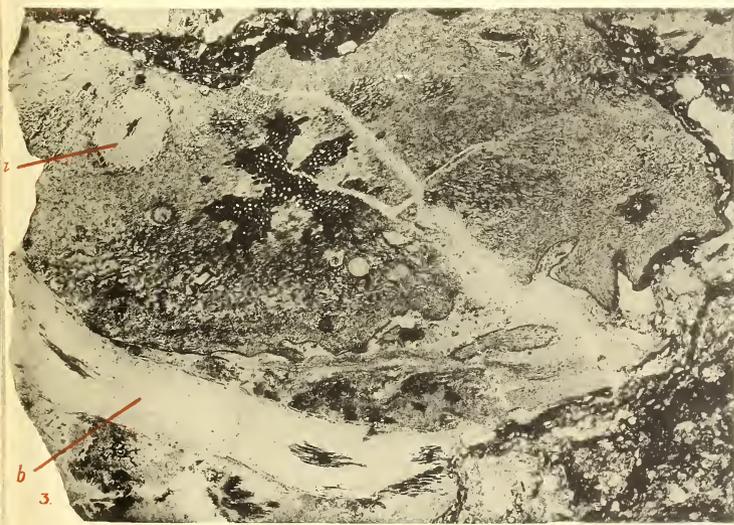
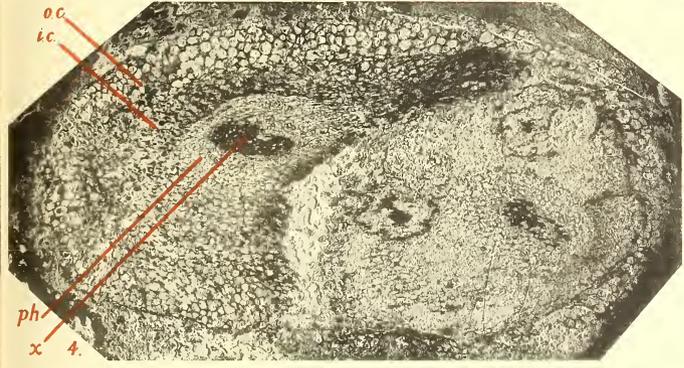
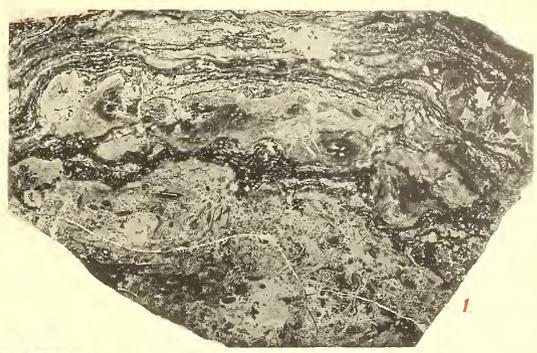
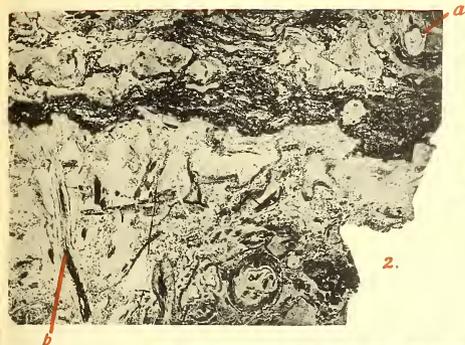
Fig. 124. Another sporangium in longitudinal section, only the epidermal layer persisting. X, place of dehiscence.  $\times 33$ . (No. 2508.)

Fig. 125. Overlapping portions (*a* and *b*) of the epidermal layer from the region of dehiscence of a crushed sporangium.  $\times 105$ . (No. 2508.)

Fig. 126. Portion of the peat including at *s* a sporangium cut longitudinally. *a*, peculiar axis giving off branches as in fig. 120; *b*, strand of *Asteroxylon* tracheides.  $\times 33$ . (No. 2506.)

Fig. 127. Spores from the sporangium in fig. 123.  $\times 160$ . (No. 2513.)

We have again to gratefully acknowledge our indebtedness to the Executive Committee of the Carnegie Trust for a grant to defray the cost of the plates illustrating this memoir.

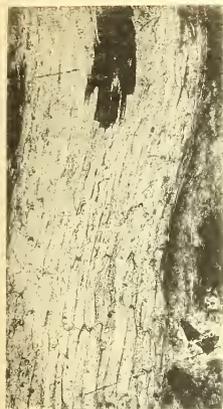


2. Kidston, Photo.

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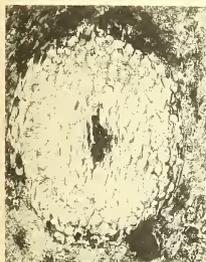
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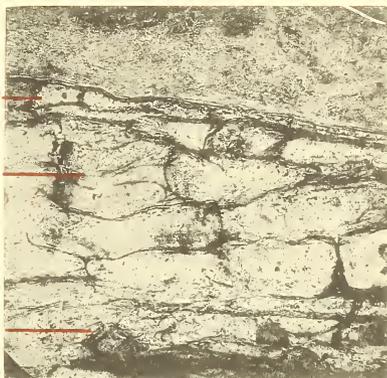
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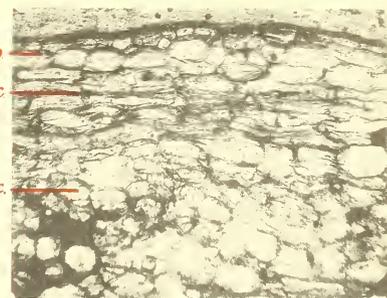
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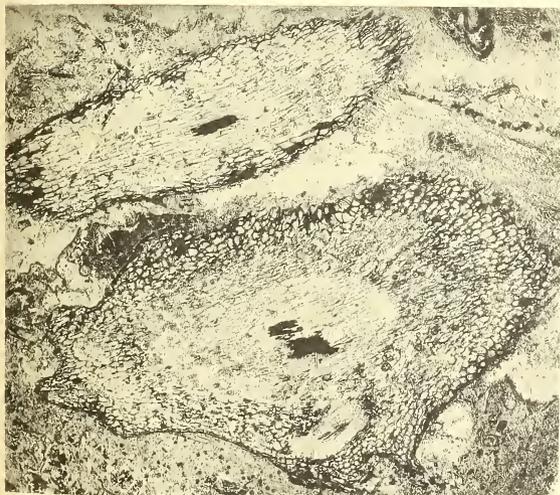
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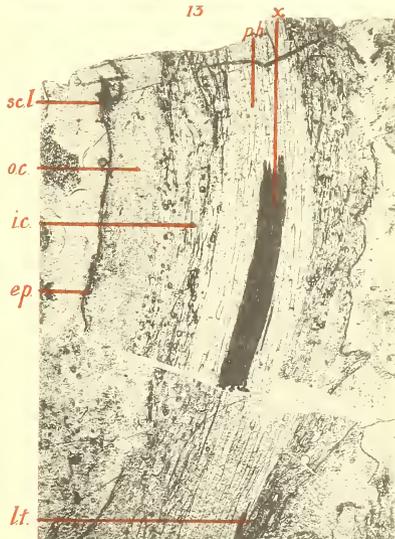
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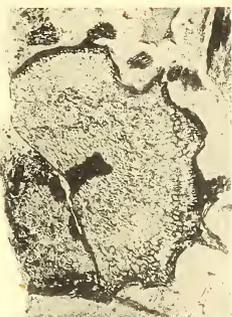
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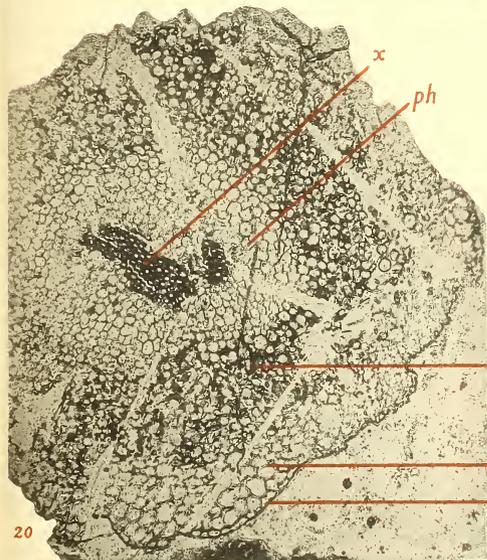
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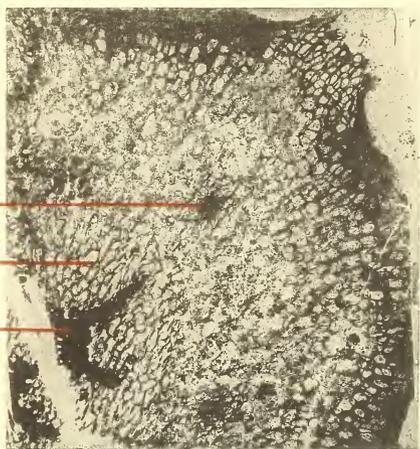
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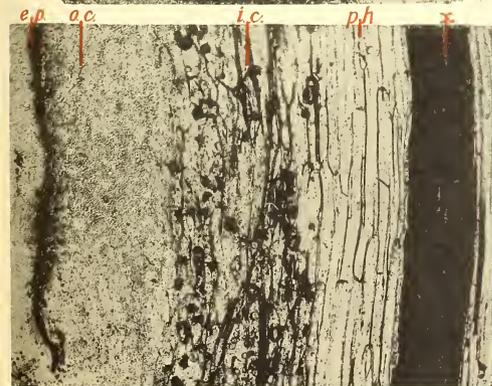
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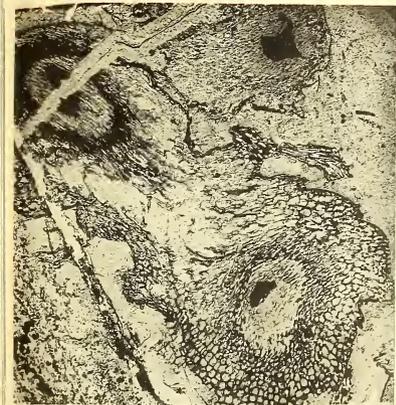


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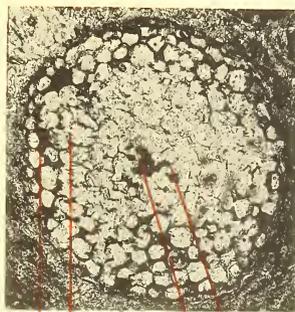


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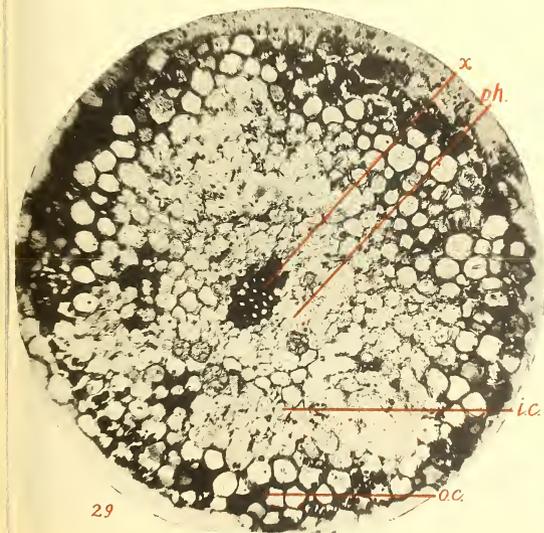
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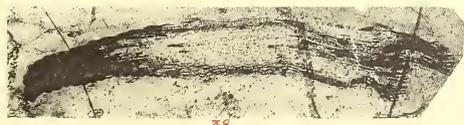
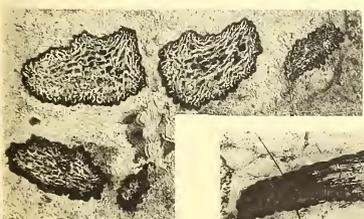
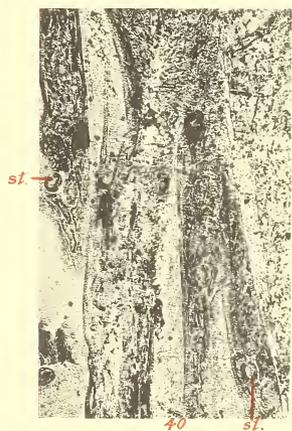
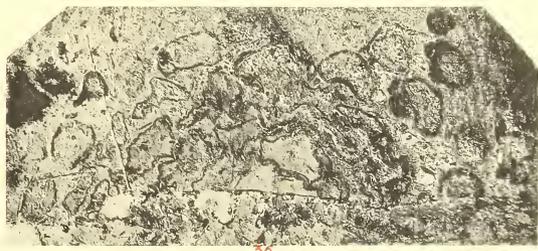
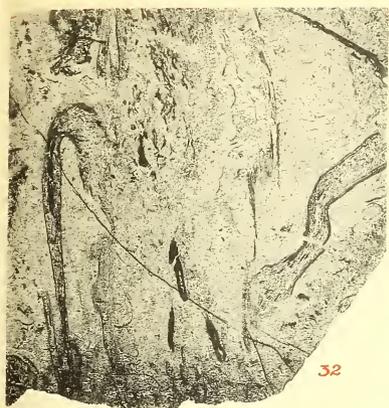


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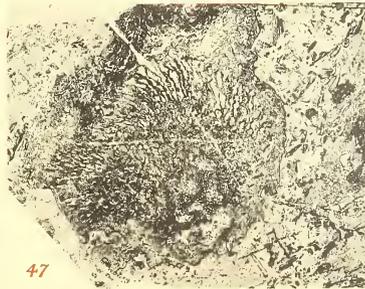
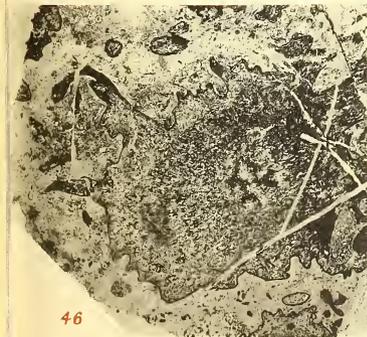
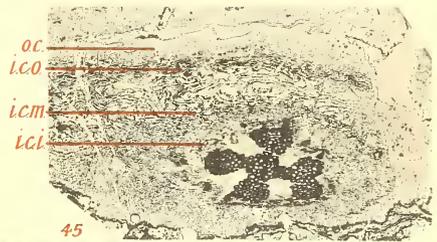
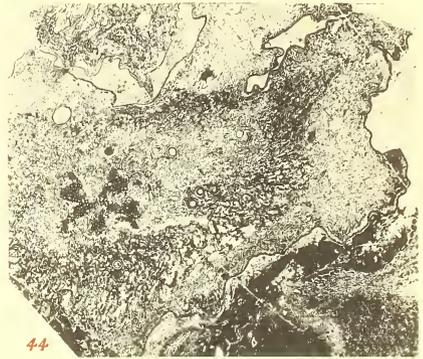
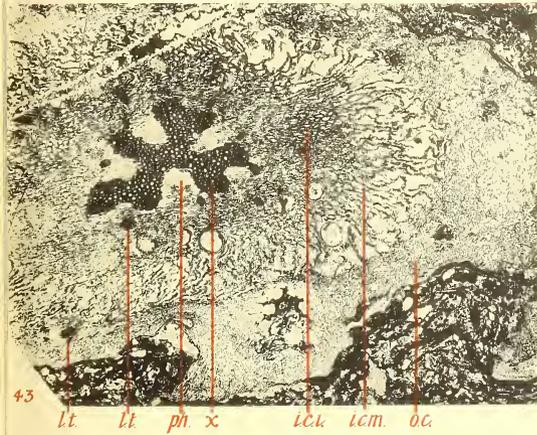
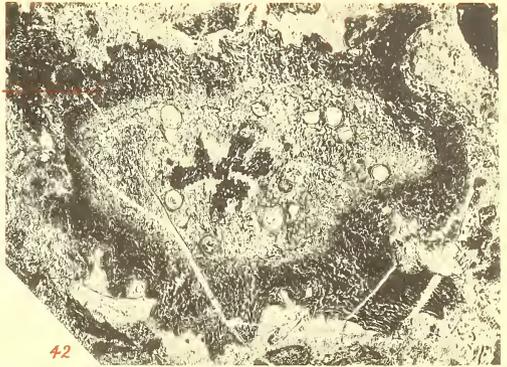
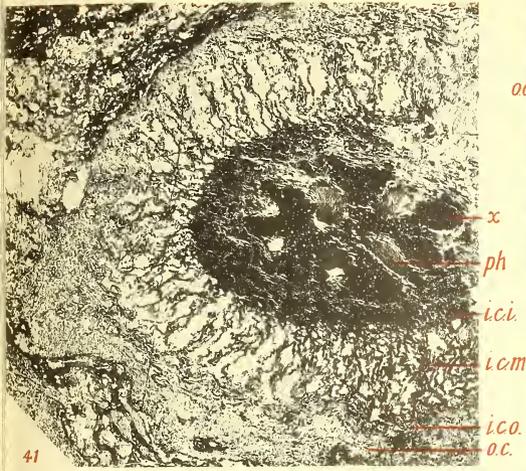


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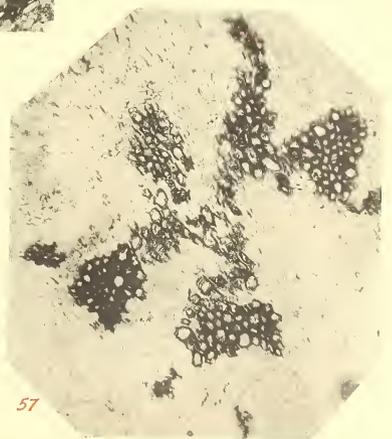
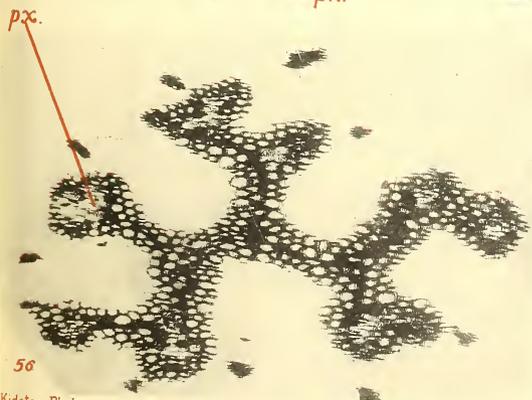
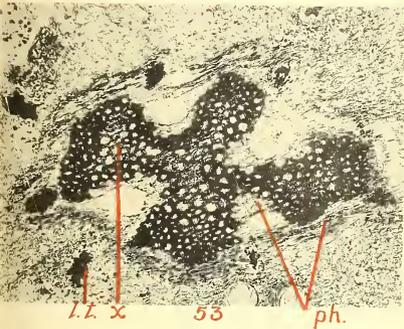
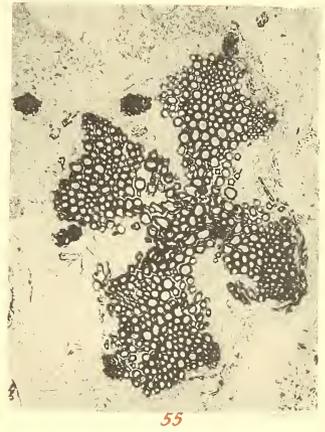
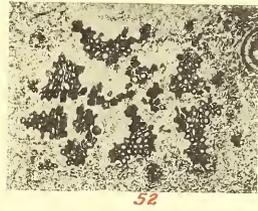
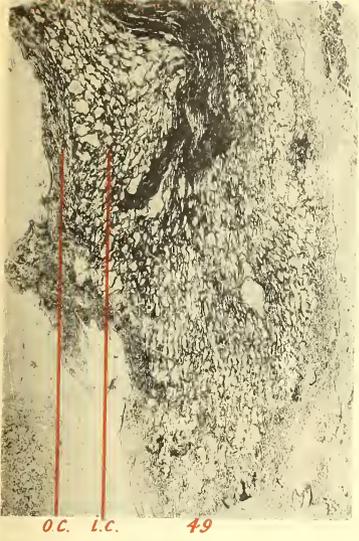
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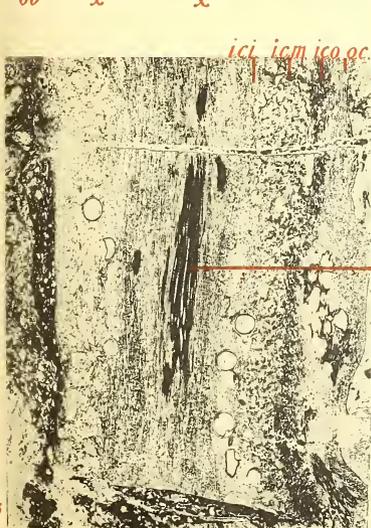
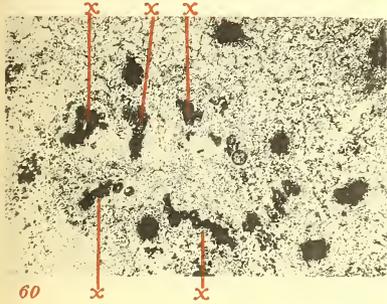
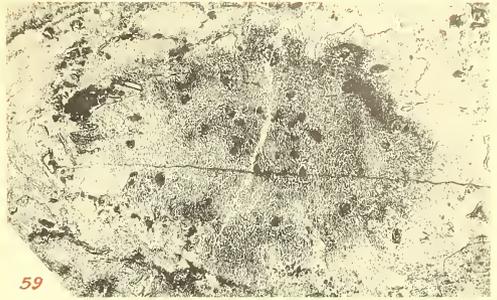
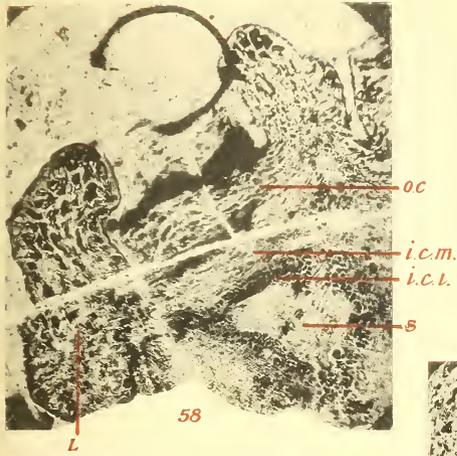


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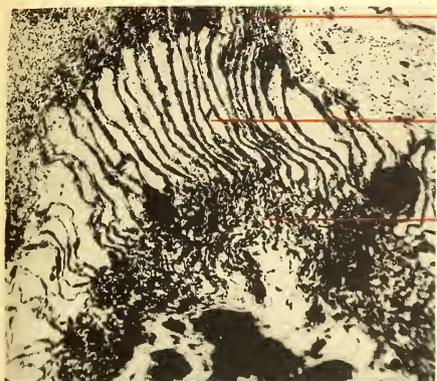
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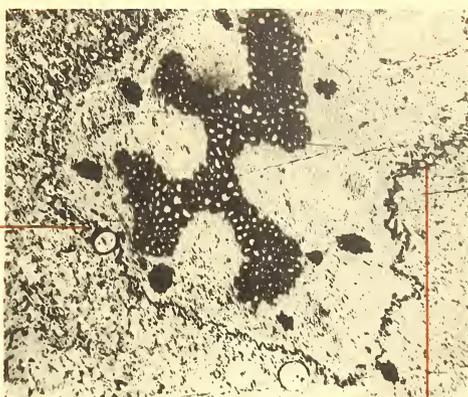






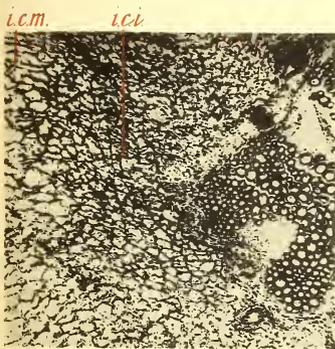


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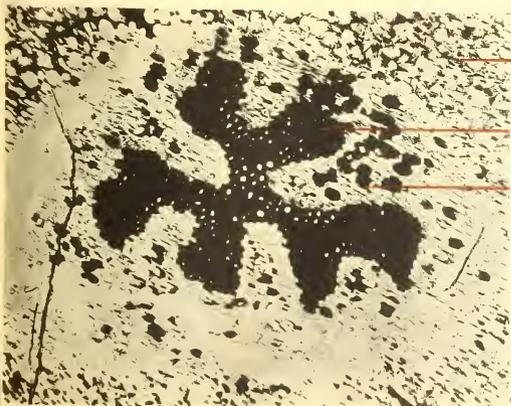
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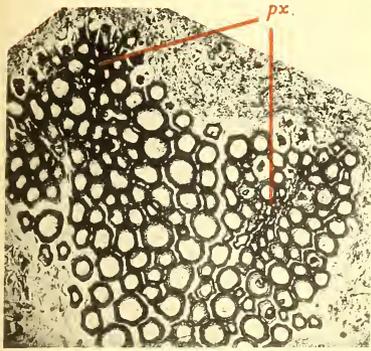
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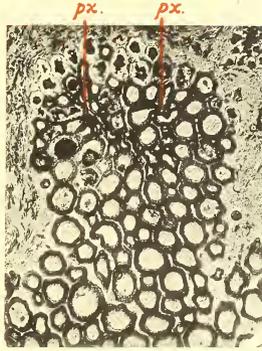
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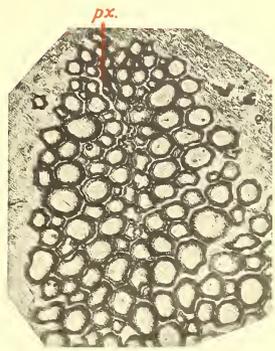




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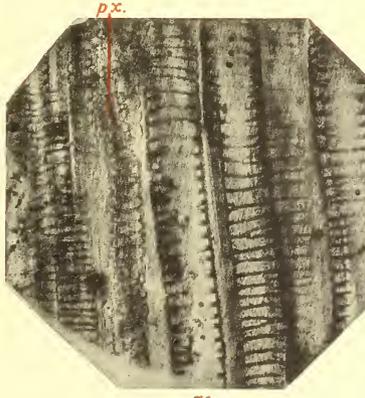
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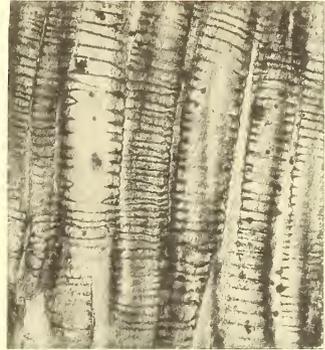
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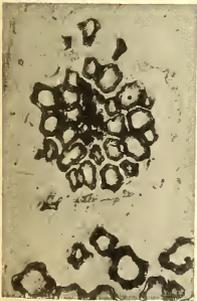
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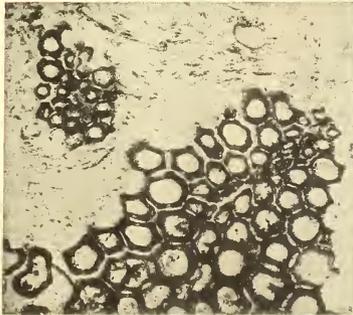
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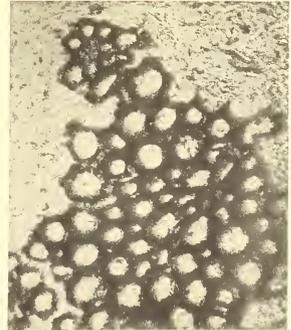
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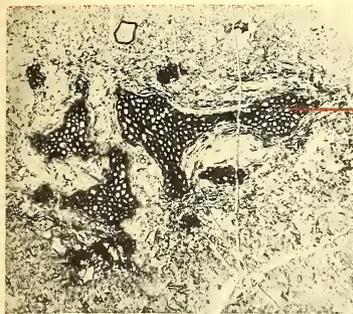


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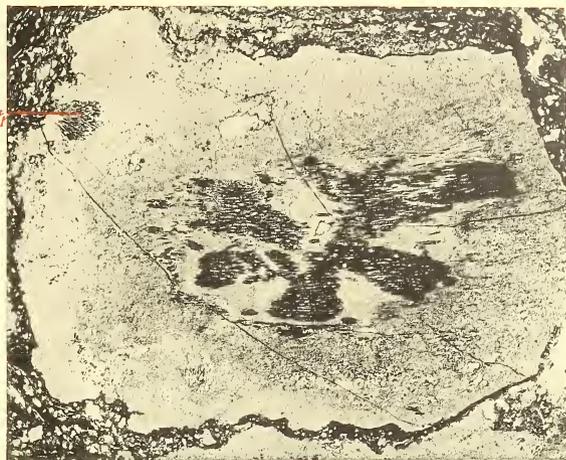


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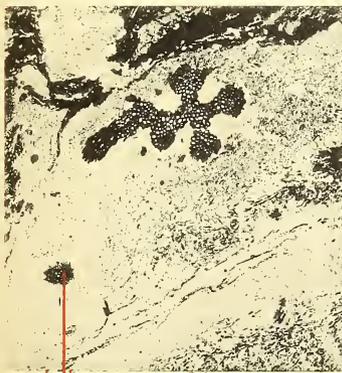




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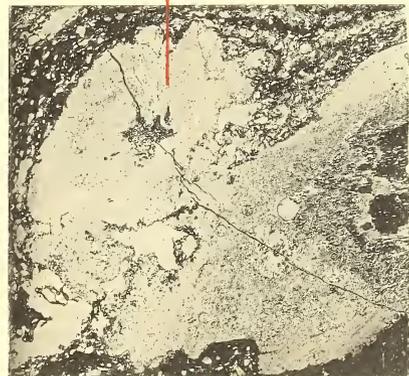
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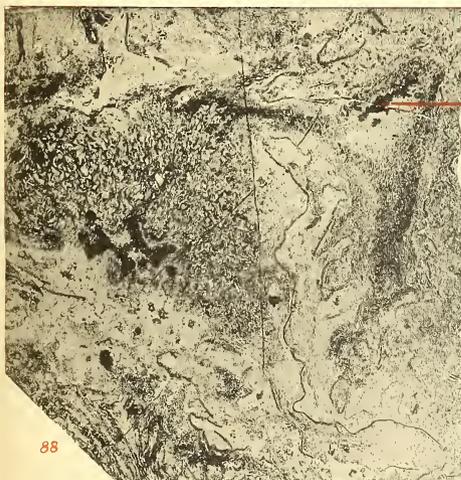
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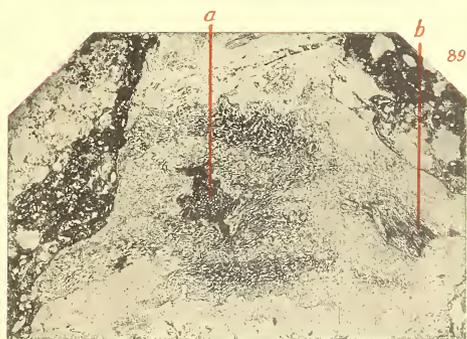
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R. Kidston, Photo.

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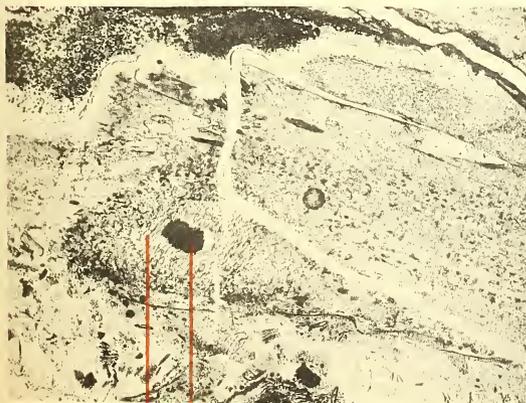
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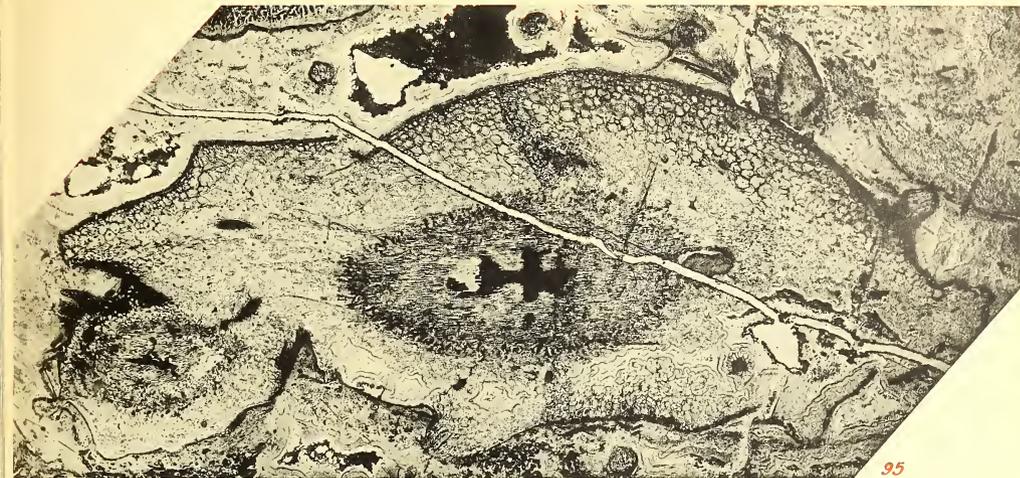


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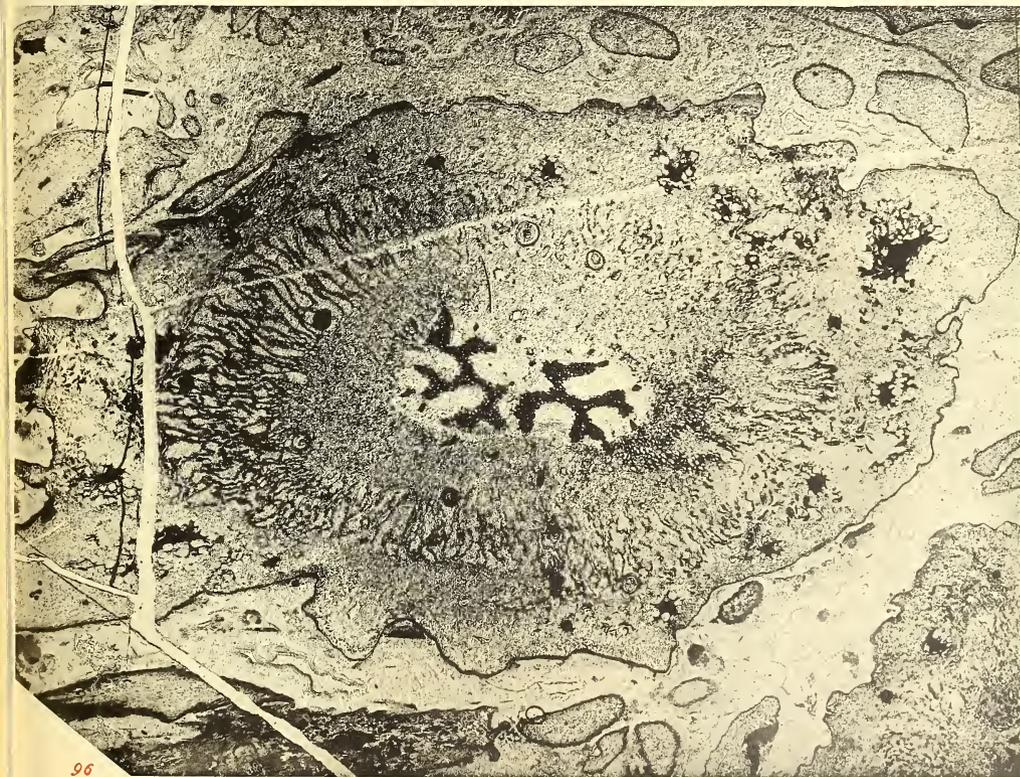


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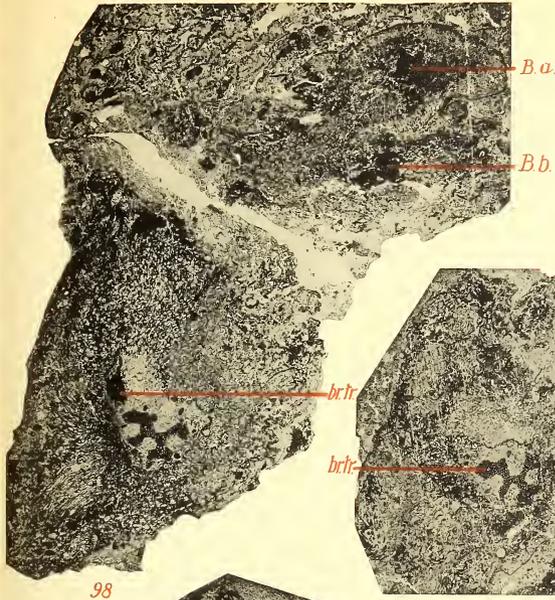
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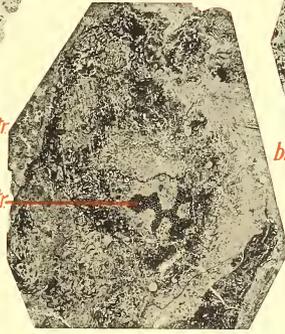
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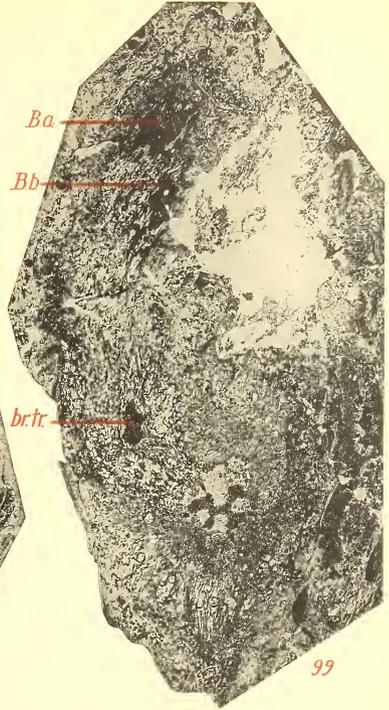




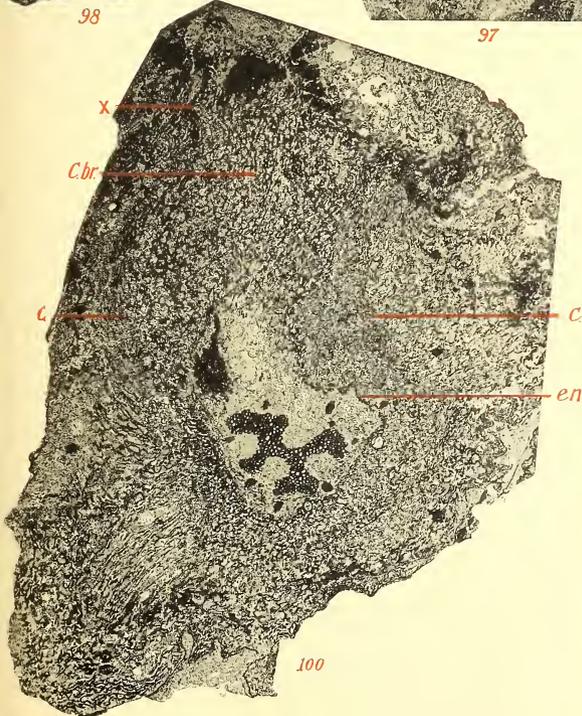
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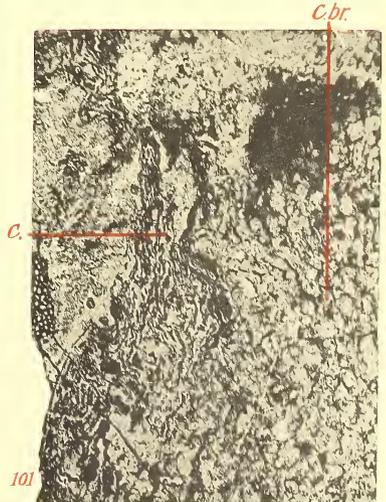
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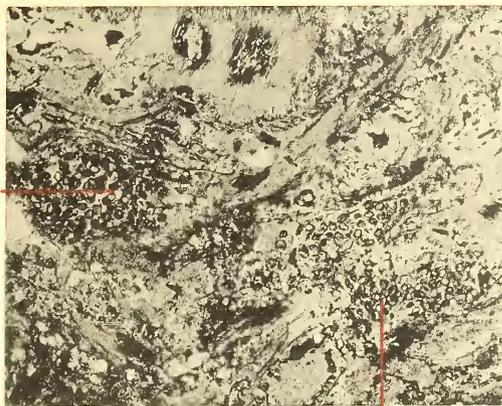
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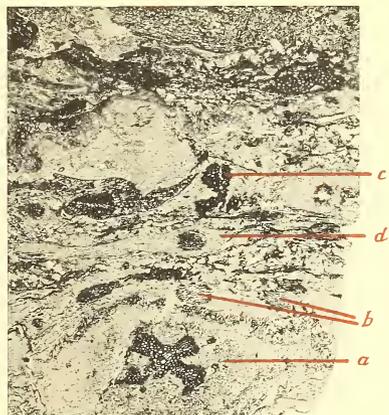




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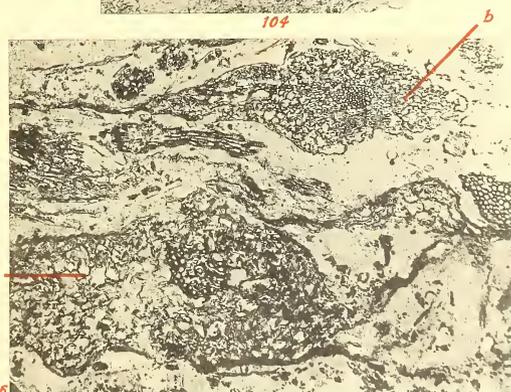
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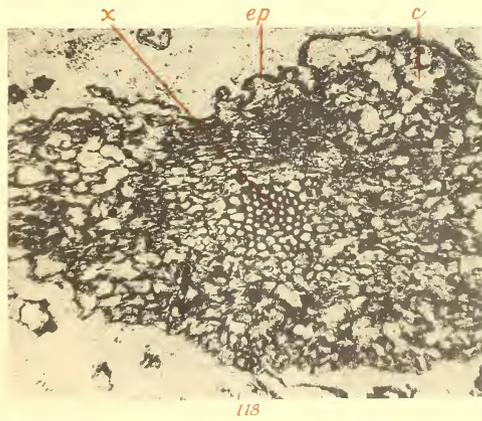
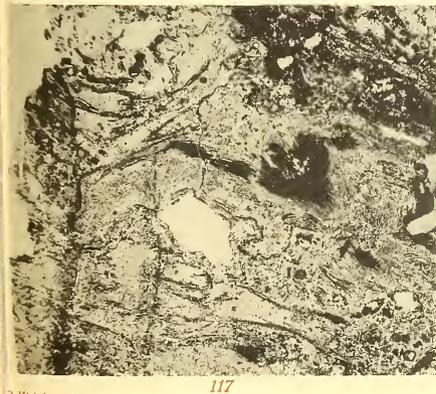
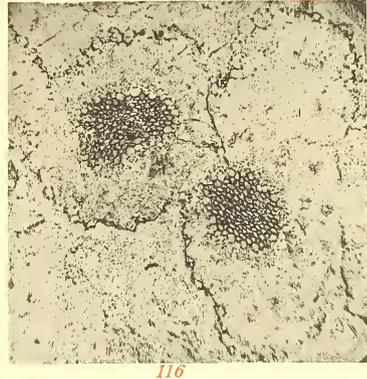
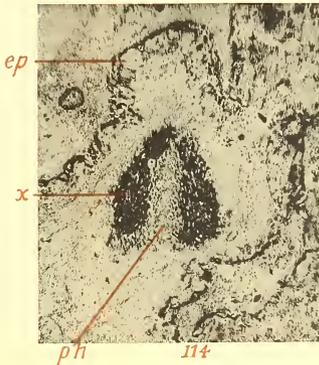
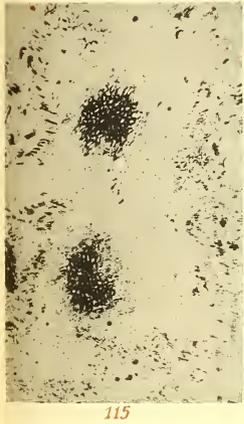
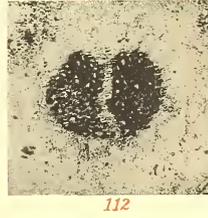
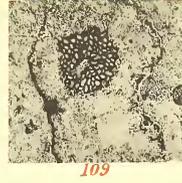
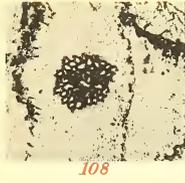


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R. Kidston, Photo

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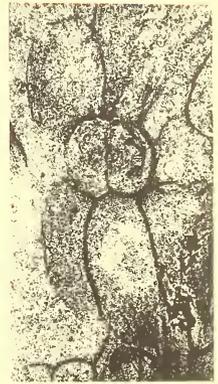




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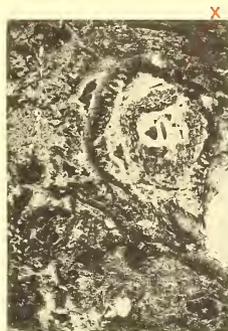
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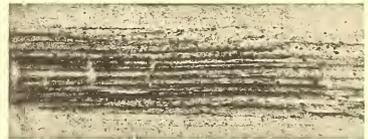
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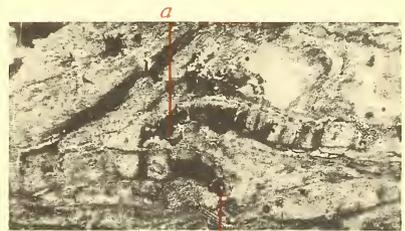
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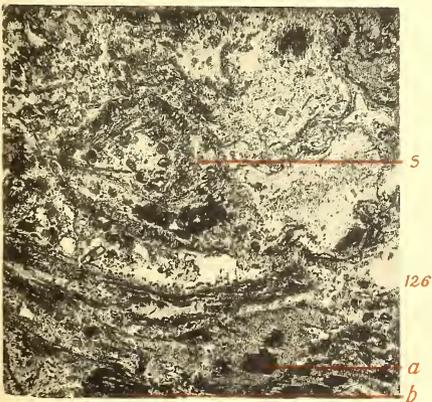
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XXVII. Pt. 1	0 16 0	0 12 0	" Pt. 3	1 10 0	1 3 0	" Pt. 3	1 10 0	1 2 5
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XXXIV. 2	2 0 1	1 11 0	" Pt. 4	0 4 6	0 3 6			

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# TRANSACTIONS

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## ROYAL SOCIETY OF EDINBURGH

VOLUME LII, PART IV.—SESSION 1920-21.



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XXVII.—**Scottish National Antarctic Expedition, 1902-1904: Cambrian Organic Remains from a Dredging in the Weddell Sea.** By **W. T. Gordon, D.Sc.**, Reader in Geology, University of London, King's College. (With Seven Plates.)

(Read March 13, 1915. MS. received December 4, 1919. Issued separately June 9, 1920.)

INTRODUCTION.

From a biological point of view considerable interest must always attend any investigation of the earliest known organisms, and, although we may legitimately infer that a flora and fauna existed prior to Cambrian times, the organisms preserved for us in rocks of that age constitute, at present, the first chapter of palæontological history. For this reason alone the Archæocyathinæ are important, since they form part of the Lower Cambrian fauna. When, however, we consider that the genera included in the group are very distinct from one another (indicating that the family was probably of considerable antiquity even in those early times), that the types have, as far as we know, a wide geographical distribution, and that to certain skeletal characters usually associated with the Porifera they unite others more common among the Cœlenterata, interest is still further stimulated. On the other hand, although recorded in great abundance from several widely separated localities, they are not, as a rule, common fossils in Cambrian strata, and consequently the group has not received much attention.

The investigation of such specimens as have been obtained has been carried on along very different lines by the several authors who have studied them, and consequently it is often a matter of no little difficulty to correlate specific diagnoses. Thus BORNEMANN\* based his specific determinations, to a large extent, on external shape, and to that end employed thin sections of the specimens, not necessarily cut in any particular direction through the organism. TAYLOR † employed several features in his diagnoses, chief among which is the diameter of the pores which form such a marked feature in all the skeletal elements. It is only fair to state that BORNEMANN also refers on occasion to the pores, but in this respect the plates which illustrate the memoir are more useful than the text. By a careful measurement of his photographs, a fairly accurate idea of the porous structure may often be obtained, even although it is not specially mentioned in the text.

The method of investigation has depended greatly on the mode and state of preservation. Where the specimens are weathered out from the matrix, direct

\* BORNEMANN, "Verstein. Sardinien," *Novo Acta der Ksl. Leop.-Carol. Deut. Akad. der Nat.*, vol. li and vol. lvi, Halle, 1886, 1891.

† TAYLOR, "Archæocyathinæ from Cambrian of South Australia," *Mem. Roy. Soc. S. Australia*, vol. ii, pt. ii, 1910. TRANS. ROY. SOC. EDIN., VOL. LII, PART IV (NO. 27). 106

measurement was possible; where the skeletal structures were preserved in silica in a calcareous matrix (as in the South Australian types described by TAYLOR), the details were etched out by means of acid; where the skeletons were enclosed in the matrix, thin sections or polished sections were employed. There is little doubt that the preparation of thin sections is the best means to elucidate the minute details, but there are difficulties, as pointed out by HINDE,\* in obtaining a proper orientation of such sections. This is seen in a marked degree in BORNEMANN'S memoir, where many of the figures are from very oblique sections.

In the present instance the material was very scanty, and to prevent waste small sections of individual specimens were prepared. With a certain amount of care in the orientation of these, it has been possible in most cases to show the following characters:—

- (a) The nature of the fixation of the skeleton to the substratum.
- (b) The appearance in cross-section at or near the top of the specimen.
- (c) The size and arrangement of the pores on the walls, septa, and tabulæ.

As mentioned above, the material was not abundant, and in some cases all these characters have not been observed. In certain genera emendations have been made on the descriptions of species already recorded, and a few new species have been added to the group.

Before passing to a detailed description of the forms examined, it is necessary to devote a word or two to the material investigated and the locality from which it was obtained. All the specimens were enclosed in small pieces of a white limestone broken from a block which was dredged from a depth of 1775 fathoms in the Weddell Sea, in lat.  $62^{\circ} 10' S.$ , long.  $41^{\circ} 20' W.$ , Station 313 (text-fig. 2, X). When the fragments were glued together, prior to being cut into sections, they formed two pieces each under a pound in weight. Both must have belonged originally to the same mass, though it is doubtful if they represented the whole of the original block, since they did not fit exactly together. This is worthy of record, as erroneous statements have been made regarding the amount of material available.† The outer crust of the fragments showed considerable weathering effects, so that a layer of white powdery material fully one-eighth of an inch thick encrusted the whole external surface.

The position in the north of the Weddell Sea from which the boulder was dredged cannot be considered as marking the position of any limestone band, for the block occurred among other debris evidently derived from a deposit of material dropped by melting icebergs. The ocean drift near the locality is to the north and east, so that the bed from which the material was originally torn must lie further into the Antarctic continent. (Other forms of *Archæocyathinæ* have been recorded from the Beardmore Glacier moraines, and were probably carried from a

\* HINDE, G. J., *Q.J.G.S.*, vol. xlv, p. 133, footnote.

† *British Association Report: Meeting in Australia*, 1914, p. 413.

point about 85° S.) No evidence has been obtained, however, as to how far to the south of 62° 10' S. we might expect to find the band from which the material was derived.

Although the specimens were dredged in 1903-4, it was not until 1913 that Dr BRUCE handed the material over to me; meanwhile Archæocyathinæ had been recorded from the Beardmore Glacier moraines by Professor DAVID, PRIESTLEY,\* and T. G. TAYLOR.† None of their specimens, however, are specifically determinable with certainty; indeed, it is open to doubt if they are generically recognisable. That they do belong to the group is perfectly certain, and two families are represented—Archæocyathidæ and Spirocyathidæ,—according to TAYLOR'S investigations.

In the present instance most of the forms are well preserved, and specific determination is perfectly easy as far as the material is concerned. The skeleton consists of granular calcite, and the matrix of rather turbid crystalline calcite. Occasionally the original skeleton has been leached out and subsequently replaced by clear crystalline material. In such cases the details of the skeletal structures may be obliterated, but in many examples the turbid matrix has remained and preserves the porous structure at least. All types of preservation are often distinctly seen in the same specimen. A section of *Coscinoocyathus enlutus* is represented in Pl. I, fig. 1. It is cut to pass vertically through the inner wall, which is shown along the centre of the figure. The outer wall with its pores occurs at *c*, while between the walls are the interseptal loculi. An examination of the inner wall at *a* proves that the original wall is present, and the pores are filled in by the cloudy matrix; but at *b* the wall has disappeared, and the space is filled with clear crystalline calcite. The pores are indicated, however, by the matrix which originally filled them in. At various parts of the same figure the outer wall, septa, and tabulæ have been similarly destroyed, but no difficulty arises in the determination of these structures.

In one or two examples exposed on the outside of the block, the less resistant character of the granular skeleton is again indicated. The pores of the outer wall are then represented by papillæ (Pl. I, fig. 2, along both sides of the skeleton in the lower part of the figure). Such papillæ are really the portions of the matrix which filled the pores, while the spaces between the papillæ were originally occupied by the granular calcite of the wall. Along the septa as at *a* of this figure the apparent pores are really where the solid portion existed, but this has been dissolved out, and the matrix is left as a continuous bridge between adjacent loculi. A similar feature may be noted across the tabulæ at *b*. Even in such cases, however, no difficulty occurs in interpretation.

In addition to the remains of Archæocyathinæ, other organisms are represented in the limestone. Fragments of shell and the carapace of trilobites occur, but

\* *Compte rendu du XI<sup>e</sup> Congrès Géologique International*, 1910, p. 774.

† *British Antarctic Expedition*, 1907-9, "Geology," vol. i, pp. 235 *et seq.*

clusters of bifurcating tubules referable to the Algæ often occupy the greatest bulk of the rock. Indeed, it would more properly be called an algal limestone containing Archæocyathinæ, etc. More important than the shell and trilobite fragments are spicula probably referable to the Porifera. They are not abundant, nor are they well preserved, but they compare very well with similar spicules from the Beardmore Glacier moraines, as will be seen later.

#### DETAILED DESCRIPTION OF THE SPECIMENS.

### PLANTÆ.

#### Algæ.

EPIPHYTON, Bornemann, 1886.

*Epiphyton fasciculatum*, Chapman.

1910. *Solenopora?* Priestley and David, "Notes on British Antarctic Expedition, 1907-9," pp. 775-777, fig. 7, *Compte Rendu du XI<sup>e</sup> Cong. Géol. Inter. Stockholm*.

1914. *Epiphyton flabellatum*, Chapman, David, and Priestley, *Report of the British Antarctic Expedition*, "Geology," vol. i, p. 241.

1916. *Epiphyton fasciculatum*, Chapman, *Report of the British Antarctic Expedition*, "Geology," vol. ii, pp. 81-83.

The most common fossil in the material consists of clustered groups of small radiating and bifurcating tubules (Pl. I, fig. 4, *a*). In transverse section the tubules are circular and sometimes closely adpressed. As a result a typical section is very similar to that shown in Pl. I, fig. 16, and the identity of this form with that figured by PRIESTLEY and DAVID from the Beardmore Glacier moraines is apparent when we compare this figure with that published by these authors under the name of a "Solenopora-like organism." A close examination of their figure shows that the tubules bifurcate, and a similar phenomenon is clearly indicated in the present material (Pl. I, figs. 3, 4, and 4*a*). In the last two figures, at *a*, repeated dichotomy of the thallus and the swollen ends impart a distinctly fucoid appearance to the whole. Indeed, the algal form of this type is much more pronounced than in any *Solenopora*. The nearest approach to the form is probably *Ortonella*, as described by Professor GARWOOD from the Carboniferous Limestone of North-West England.

CHAPMAN has examined the material from the Beardmore Glacier in more detail, and in the *Report of the British Antarctic Expedition*, 1907-9 ("Geology," vol. i, 1914), has correlated it with *Epiphyton flabellatum*, Bornemann; but in a later contribution ("Geology," vol. ii, 1918), has described it under a new specific name, *E. fasciculatum*, and given three figures. These figures are not very good, but the description and measurements leave no doubt but that the form recorded here is identical with the Beardmore Glacier type.

*Epiphyton grande*, sp. nov.

An occasional group of a much larger algal form occurs with *Epiphyton fasciculatum*. The relative size is clearly seen in Pl. I, fig. 3, when we compare *b* with *a*. In the former type the tubule is about twice the diameter of that in *E. fasciculatum*, and the distance between the bifurcations is also greater. Consequently a much more lax appearance is imparted to the whole thallus. Another specimen is represented in Pl. I, fig. 5, and here the branching character is particularly well exhibited. Occurring under precisely the same conditions as *E. fasciculatum*, the idea that we have here merely more robust examples cannot, I think, be admitted. If it were so, we should expect to find intermediate forms; but only the two sizes of tubule occur. One is reminded in this connection of the two sizes of tubule in *Micheldeania*, but, in that genus, the two forms occur intergrown with one another, and not distinct and separate as in this case. While, therefore, one has a certain diffidence in erecting a new species where size is the chief diagnostic character, one feels that it is justifiable here. The new species, then, has tubules twice the diameter of those in *E. fasciculatum*, and the bifurcations are twice to three times as far apart as in that species, so that either in transverse or longitudinal section the grouping is less compact.

Compared with *E. flabellatum*, Bornemann, the new form is very similar as regards diameter of tubule. Indeed, taking CHAPMAN'S figures, *E. flabellatum* comes between *E. fasciculatum* and *E. grande* as regards this measurement. A greater distinction is visible when we consider the bifurcations. In *E. flabellatum* and *E. fasciculatum* the bifurcations are close together and only differ in minute detail, while in *E. grande* the dichotomies are further apart and as a consequence the whole tuft presents a much more lax appearance.

There are now three species of *Epiphyton* recorded from Cambrian rocks, all closely similar and quite distinct from any other alga yet recorded. VON TOLL'S *Confervites primordealis*, Bornemann, from Siberia, seems almost certainly an *Epiphyton*, but details are lacking which would assist in placing the specimens in any of the above categories.

## ANIMALIA.

## Porifera.

Spicules probably referable to this group occur occasionally in the sections, but unless the plane of section happens to pass through or near the point of junction of the various rays it is difficult to determine the precise type of spicule. Then again the original material has been removed in every case and casts in crystalline calcite have been formed.

The most common type is that represented in Pl. I, figs. 8 and 9. The spicule is large and the rays seem to unite in a flat head slightly domed in the centre

(figs. 8 and 9, *a*). The number of rays present in any example is small, but the angle of divergence between them is such that the complete spicule was probably heteractinellid. They are similar in size and appearance to those recorded by TAYLOR from South Australia and from the moraines of the Beardmore Glacier.

Another multi-rayed example is seen in Pl. I, fig. 6, and again the complete form is rather difficult to determine. It had certainly not fewer than six rays, but it could not be a hexactinellid spicule, since the angle of divergence of the rays cannot be reconciled with any possible section of a true hexactinellid. It might be said that a section through the centre of a hexactinellid type would approximate to the figure, but, as at least two examples have been observed both almost exactly alike, the chances are that they are sections of another type of heteractinellid spicule rather smaller than the type of figs. 8 and 9.

We pass now to consider forms of spicule which may be classified with greater ease than the above. The first of these is undoubtedly tetractinellid (Pl. I, figs. 7 and 11). In fig. 7 the plane of section is oblique, but all four rays are indicated, though only one is complete. The "calthrop" form, however, is very evident. The second figure (fig. 11) presents a much more perfect example, since the plane of section has cut through almost perpendicular to one of the rays, and the other three diverge at the normal angle in calthrop spicules. The vertical ray is indicated at *a*, where a distinct convexity appears in the angle between the two rays.

Examples of hexactinellid spicules also occur, and two of these are figured (Pl. I, figs. 10 and 14). The great characteristic of such forms is that the rays are set with respect to each other at angles which are multiples of  $90^\circ$ . Lastly, several very characteristic specimens like those shown in Pl. I, figs. 12 and 13, recall a similar example figured by TAYLOR from the Beardmore Glacier locality. His specimen certainly bears some resemblance to the spicule of the recent *Lelapia*, but it is really not such a simple form. An examination of his figure\* proves that at the base of the fork an upward projection appears, and indeed that a perfectly horizontal section through it would have looked more like that shown at *a* of Pl. I, fig. 12. This fortunate section is exactly in the plane of the spicule, and several other specimens occur in the same section. A rather poor example is seen at *b* of the same figure (Pl. I, fig. 12), where only the forked ray is visible. Another example is figured in the same plate at fig. 13, but again the plane of section has passed obliquely across the spicule. The two rays passing to the right and left of the forked one at once dissipate the resemblance to *Lelapia*, but the fact that the rays are always at right angles to one another would tend to place this form among the hexactinellids. Further, it is quite probable that rays occurred above and below, *i.e.* running perpendicular to the plane of section, in which case we may relegate the spicule to a hexactinellid type where one of the rays has become

\* *British Antarctic Expedition, 1907-9, pl. lxxix, fig. 5.*

bifid. Similar modifications are not unknown among modern hexactinellid spicules, but none quite like that of fig. 12 has ever been recorded.

The sponge remains, or at least the spicules which are probably sponge remains, thus parallel in a remarkable manner the resemblances shown among the algæ from the Beardmore Glacier blocks and the mass dredged in the Weddell Sea (positions almost opposite one another with respect to the South Pole).

### *Archæocyathinæ*, Bornemann, 1884.\*

The most important organic remains in this limestone can be definitely placed among the *Archæocyathinæ*. Several families are represented, and the different species may be grouped as follows:—

#### *Archæocyathidæ*, Taylor, 1910.†

*ARCHÆOCYATHUS*, Bellings, 1861.‡

*Archæocyathus pauciseptatus*, sp. nov.

One exceedingly small specimen is worthy of notice, since it is the only example in the material which approximates to the type of *A. profundus*, Billings. One transverse section was obtained, and it is figured in Pl. VI, fig. 63. The imperforate outer lamina on the outer wall, the straight septa, and the irregular but numerous dissepiments separate the type from *Spirococyathus*. The septa are few in number and perforated as seen in transverse and longitudinal section (Pl. VI, fig. 63, *p*, and fig. 64, *p*, respectively). The dissepimental platforms are very oblique and irregular. Their inner ends are continued across the central cavity and unite in an irregular tissue (Pl. VI, fig. 64). Smaller offsets from these help to fill in the whole central cavity. The inner wall is porous, but lack of material has prohibited a more accurate description. The only other form which approximates to the above is *A. dissepimentalis*, Taylor, but that species has more numerous septa and no tissue in the centre of the cup.

#### *THALAMOCYATHUS*, gen. nov.

*Archæocyathidæ* with septa straight, perforate or imperforate. No tabulæ or dissepiments cross the interseptal loculi. Walls simple or modified. Central cavity frequently filled by callus growth in the older part of the skeleton, *i.e.* near the base. (The greater number of the species formerly in the genus *Archæocyathus* will fall into this new division. The reasons for erecting a new genus will be discussed below.)

\* *Geol. Zeitschr.*, 1884, p. 706.

† *Mem. Roy. Soc. South Australia*, vol. ii, part ii, p. 105.

‡ *Geology of Canada*, "New Species of Lower Silurian Fossils," p. 3.

*Thalamocyathus tubavallum*, Taylor, sp.

1910. *Archæocyathus tubavallum*, Taylor, *Mem. Roy. Soc. South Australia*, vol. ii, part ii, p. 123, text-figs. 28, 29.

One small specimen from which only three transverse sections were prepared could probably be referred to this species. Although TAYLOR only obtained a small fragment of the form, its characters are fairly well marked. The inner wall is thick, and consequently the pores seem to be short pipes. The outer wall has smaller pores, and is much thinner, while the septa are imperforate. Unfortunately TAYLOR only published drawings of this form, and so correlation is difficult. One section of the present specimen is given in Pl. I, fig. 15. The thick inner wall is marked, as also are the small pores on the outer wall. The septa are imperforate, except for stirrup-pores at their inner ends. These are clearly seen at *a* and *b* of the figure above mentioned. As no longitudinal sections could be prepared, the diameter of the pores cannot be clearly seen. Those on the inner wall seem to average 7 per mm., and those on the outer wall 10 to 11 per mm. The measurements correspond fairly well with TAYLOR'S text-fig. 29.

*Thalamocyathus trachealis*, Taylor, sp.

1910. *Archæocyathus trachealis*, Taylor, *Mem. Roy. Soc. South Australia*, vol. ii, part ii, pp. 125, 126, pl. i, iii, v, viii, text-fig. 22.

Three of the specimens discovered could be referred to the above species, and, as the material allowed of examination of minute details, TAYLOR'S description of the species will be emended to some extent, and consequently the new examples must be described in considerable detail. The largest specimen was probably 2.5 to 3 cm. in length, 1 cm. in diameter at the top, and tapering gradually to a point. An oblique section near the top of the cup is shown in Pl. II, fig. 18. The great number of closely set septa is at once apparent, while the large pores of the inner wall and the small pores of the outer (notably at *a*) are also visible. In fig. 17 a much smaller specimen is represented in transverse section, and a distinct feature is the breadth of the inner wall, although in some places it has disappeared entirely. This latter feature is still more obvious in Pl. II, fig. 20, where at *a* the wall is very broad, whereas at *b* only the inner rim is visible, and the septa seem to stop far short of the wall, while their inner ends have become thickened.

The reason for all these features is indicated in fig. 20. The apparent inner wall is really a broad ring of no great thickness, and arched so that a gutter is formed on the upper surface. Should the plane of section correspond with that of the ring a complete platform is seen, but in general the broad ring is only partly coincident with the plane of section, and in the other parts the margin, or part of the margin, is alone included. (See also fig. 19.) This will be even more easily understood by reference to fig. 23, where a longitudinal section of the same specimen is represented.

Here, the outer wall—a continuous, porous lamina—is seen at *a*; and at *b* the inner wall is evidently not continuous, but a comparison of figs. 20 and 23 clearly shows that it consists of a series of broad rings set one above the other and soldered to the septa. As mentioned above, the rings are not thick and are grooved on their upper surfaces.

At *c* (fig. 23) a septum appears cut longitudinally, and near the top of the figure the attachment of four rings to this septum is shown. A longitudinal section at right angles to the plane of fig. 23 demonstrates that the pores of the inner wall are delimited by the vertical septa and the horizontal ring-platforms (Pl. II, fig. 22, *a*). This figure represents the vertical septa at *d* crossed by the horizontal platforms *b*, the spaces between the intersections constituting the pores (*a*). Such pores ought to be square in section, but increased growth at the fused corners, and to a certain extent all round the pores, has given a circular shape to the aperture. Such increase in thickness of the septa in this region accounts for the swollen inner ends so apparent at *a* in fig. 19. Reverting to fig. 22, however, it seems difficult at first sight to determine which are the septa and which the ring-platforms, but a closer examination soon indicates a means of distinction even in such a section. At *c* in that figure, and again at *a* in fig. 19, a series of small dots may be noted which are in each case continuations of the platforms. The explanation of this row of dots is given by fig. 23, where (at *b*) on the under surface of each platform a small projection is shown. Now, turning again to fig. 19, the origin of the row of dots is quite clear. They represent a series of small peg-like projections or denticles on the under surface of each platform. They are again shown, more highly magnified, in Pl. III, fig. 26, where at *a* the denticles are very evident, at *s* the swollen end of a septum is equally so, and at *p* a septal pore is conspicuous. The denticles are so close together that in the thickness of a section more than one would be included, or, to put it otherwise, no section could be cut thin enough to pass between two denticles; consequently any longitudinal section of the ring-platforms will always show the denticle on the lower surface of each.

Unfortunately, such a characteristic feature is not mentioned by TAYLOR in his original description of the species, but this was due to the method he employed of etching the skeleton out by dissolving the matrix in hydrochloric acid. Such minute denticles were broken off. That such must have been the case is shown in Pl. II, fig. 24, where a longitudinal section is represented which was prepared from material kindly given me by Mr TAYLOR some years ago. The identity of this type with that of fig. 23 is undoubted. At *b*, in each, the denticles are shown, at *c*, a porous septum, and at *a*, the finely porous outer wall. It is true that the Australian specimen is distinctly more robust and larger (a point which will be referred to later), but there is no doubt that the two are specifically identical.

So far the pores on skeletal members other than the inner wall have only been mentioned incidentally: it remains to examine the porous structures in more detail. On the outer wall the pores are much smaller than those on the inner, there being 8 per mm. as compared with 5 per mm. On the outer wall the pores are arranged in rows, two or three to the interseptum, but they alternate in the rows, and thus an hexagonal outline is impressed on each individual pore (Pl. II, fig. 21).

Although only a rather oblique section of a septum has been obtained, it will suffice to give some idea of the arrangement and size of the septal pores. These latter seem (Pl. II, fig. 23) to run in vertical lines, but rather more irregularly than the pores of the inner wall. That these apertures are not in absolutely parallel rows may be proved by reference to transverse sections (Pl. II, fig. 20, *e*), where the pores on one septum are not exactly opposite those on its neighbours. As compared with the Australian specimen represented in fig. 24, the arrangement of pores is identical. In every particular except size this type agrees with *Thalamocyathus trachealis* as described by TAYLOR or shown by the section of his material which is figured (Pl. II, fig. 24).

In one particular, however, these new forms differ from the Australian species with which I have grouped them. That is the occurrence in the interior of the cup of a coralloidal type of infilling material. The resulting tissue is very evidently connected with the inner walls (Pl. II, fig. 25), and similar material has only been recorded in a few types. BORNEMANN, HINDE, and TAYLOR have each noted such a feature in some type or another, but only in TAYLOR'S *Somphocyathus* does it become prominent. In that latter genus the general form (coralloidal) is quite comparable with that discovered in *T. trachealis*. The tissue has been noted in two examples, and in each was found near the base of the cup. As will be seen later, a similar infilling has been observed in practically all the Weddell Sea specimens; it only occurs near the base of the cup; it differs in type, and so may be diagnostic in value, but, from the position in which it occurs, I am inclined to consider it a gerontic feature, since wherever it has been noted it is always present in a region where the walls are thickened and the pores more or less closed by callus growth.

No evidence of rooting processes has been obtained. In the lowest section available the diameter was 9 mm. and there were 12 septa, but it could not have been far above the extreme point, and any processes below this level could not have been very effective in balancing the whole cup. It may be that the form had no special rooting processes. As regards details of measurement, the largest specimen was 25 to 30 mm. in length, tapering to a point. The "intervallum coefficient," *i.e.* the ratio of width of intervallum to width of central cavity, has been found of little use. In Pl. II, fig. 17, it is 1/1; in Pl. II, figs. 20 and 25, 1/1.5; in Pl. II, fig. 18, 1/4.

An emended description based on the above new facts is as follows:—Cup, in small specimens, a tapering cone, in larger forms more cylindrical. Constrictions



wall has 6 rows of pores per interseptum, which is .5 mm. wide.\* Thus there are 10-12 pores per mm. on the outer wall. The septa also are porous.

The Antarctic specimen has 7 pores per mm. on the inner, and 10 pores per mm. on the outer wall; the septa are porous, and the general shape seems to conform to that of the Sardinian species. All these characters confirm the reference of the type to *T. ichnusæ*. Since both *T. infundibulum* and *T. ichnusæ* are represented by single specimens, and by single sections of these examples in each case, the specific features have been a matter of deduction rather than observation. The clearest evidence is the size of pore, and unfortunately BORNEMANN laid little stress on this point. Yet it is probably much more constant and important than the external shape, a character often rendered useless by distortion. Indeed, some re-examination of the Sardinian types is urgently required.

*Thalamocyathus flexuosus*, sp. nov.

Under the specific name of *sinuosus*, BORNEMANN † has described a *Thalamocyathus* type with narrow intervallum and characteristic plicated outline in transverse section. A well-marked feature in addition to the habit is the presence of large pores on the inner wall and small ones on the outer, there being 3 per mm. and 10 per mm. respectively. ‡ The great difference in size is also seen in other figures illustrating the work.

A rather similar form occurs in the Weddell Sea material, as a number of small fragments but no complete cup has been obtained. As a result of the flexuous outline (Pl. III, fig 27, *a*), it has been a matter of some difficulty to determine which is the outer and which the inner wall. The intervallum is narrow—about .5 mm.—and as the septa are also closely set the interseptal loculi are nearly square in transverse section (Pl. III, fig. 27). On account of the exceedingly narrow intervallum no very good longitudinal sections of the wall could be made in series, but the two figured (Pl. III, figs. 28 and 29) are from successive sections, and illustrate in some way the porous character of the walls. The first point to be noted is that the pores are almost equal on each wall, a feature only recorded so far from specimens of Australian origin—the “equivallum” type of TAYLOR. By measurement, however, it is found that on one wall the pores number 6 per mm., and on the other 8 per mm., so that a slight difference does occur. Another point of difference lies in the fashion in which the septa meet the two walls. In one case—that with the smaller pores—the septa meet the wall *between* rows of pores (Pl. III, fig. 29, *s*), but they meet the other wall along a pore-row, *i.e.* there are “stirrup”-pores, the one perforation allowing communication from the exterior to two adjacent loculi (Pl. III, fig. 28, *b*). The septa appear to be imperforate apart from the stirrup-pores at their ends. Since

\* BORNEMANN, *loc. cit.*, p. 55.

† BORNEMANN, *loc. cit.*, p. 57; and *Geol. Zeitschr.*, 1854, p. 704.

‡ Calculated by measurement from BORNEMANN, *loc. cit.*, Taf. xii, figs. 6a, 6b.

the wall with the stirrup-pores has also the larger apertures, I incline to regard it as the inner, and that with the small pores as the outer. As mentioned above, no complete cups have been obtained, but the fragments exceed in length any other form present in the material. Even if the broken specimen of fig. 27 had been complete, it would have constituted the largest specimen in the whole of this collection.

The species may be described as follows:—Walls folded gently; intervallum narrow (5 mm.). Outer wall simple, porous, pores 8 per mm. Inner wall simple, pores 6 per mm., “stirrup”-pores on inner ends of septa. Septa imperforate except for stirrup-pores.

### Spirocyathidæ.

SPIROCYATHUS, Hinde, 1889.\*

*Spirocyathus atlanticus* (Billings, sp.).

1861. *Archæocyathus atlanticus*, Billings, *Lower Sil. Fossils*, p. 4, figs. 1-3.  
 1865. “ “ “ “ *Palæ. Fossils*, vol. i, p. 5, fig. 5.  
 1880. “ “ “ “ Roemer, *Lethæa Geognostica*.  
 1886. “ “ “ “ Walcott, *Bull. No. 30, U.S. Geol. Surv.*, p. 75.  
 1889. *Spirocyathus* “ “ Hinde, *Q.J.G.S.*, vol. xlv, p. 136, pl. v, figs. 8-10.  
 1889. “ “ “ “ Walcott, *10th Annual Report, U.S. Geol. Survey*.  
 1899. “ sp., Von Toll, “Sibir. Camb.,” *Mem. Acad. Imp. des Sc. Petrograd*, ser. viii, vol. viii, p. 45, pl. vi, fig. 8.  
 1910. “ *radiatus* Taylor, *Mem. Roy. Soc. S. Australia*, vol. xi, part ii, p. 147, text-fig. 35.  
 1910. “ *irregularis*, Taylor, *Mem. Roy. Soc. S. Australia*, pp. 148, 149, pl. xvi, figs. 93, 94.

Two examples of the above form were discovered in the material, and each was about 20 mm. in length. A transverse section, fairly high in the cup, is given in Pl. III, fig. 32, and it compares well with the figures of the type specimen as given by HINDE. As in that specimen, the skeletal structures have been thickened by a coating of material, and the appearance is analogous to that produced on the septa of many rugose corals (cf. *Aulophyllum*) by “callus” growth. But the chief points of interest in these new specimens lie in the nature of the fixing organs or processes, and in the apparent similarity to the genus *Protopharetra* which is shown by the lower parts of the cup.

A cross-section at a lower level in the skeleton is shown in Pl. IV, fig. 39, and the whole is very suggestive of a section from a *Protopharetra* type. In this connection it is interesting to recall HINDE's words when describing the new genus *Spirocyathus*. He notes that he has “considerable difficulty in determining whether *Spirocyathus* could be established as a genus distinct from *Protopharetra*.” † BORNEMANN, in erecting the new genus *Protopharetra*, considered that it was not an independent type, but merely the lower part or rooting part of other forms of

\* HINDE, *Q.J.G.S.*, vol. xlv, 1889.

† HINDE, *loc. cit.*, p. 138, footnote.

the Archæocyathinæ.\* A consideration of the specimens now figured indicates that the early stages in *Spirocyathus* and *Protopharetra* are very similar; but I believe they can be distinguished, and hold with TAYLOR† that they may be independent forms belonging to the same group.

In the above-mentioned figure (fig. 39) there is another important feature, namely, the occurrence at *a*, *b*, and *c* of small structures not unlike the cup itself, except that there is no central cavity. The structure at *b* is in continuity with the thickened wall of the cup, but the others are separated from it. Similar continuity between such a strand and the cup is indubitable in Pl. IV, fig. 40, *a*. These constitute the rooting processes of this form. Here (fig. 40) the *Spirocyathus* character is very evident in the cup, and it is the second section above that of fig. 39. The lower half of this figure still shows a remarkable resemblance to *Protopharetra*, but the upper part to *Spirocyathus*. Even in Pl. IV, fig. 41, the *Protopharetra* affinities are still marked, though the regular septa near the inner wall place it with *Spirocyathus* cf. *S. irregularis*, Taylor. Pl. IV, fig. 37, shows a section at a still higher level in the cup, and the relation to *Spirocyathus atlanticus* is now evident, although, in parts, the *Protopharetra* character persists. The central cavity in figs. 39, 40, and 41 is crossed by irregular strands which are clearly outgrowths from the inner wall and continuous with the septa.

The porous nature of the inner wall is shown in Pl. IV, fig. 42, *a* and *b*. (The figure is really on its side; *a* is the top and *b* the bottom of the section.) The central cavity is cut obliquely, so that the inner wall on the one side is exposed on the right-hand side of the figure, and again at a higher level on the left-hand side. The pores are evidently hexagonal in outline (*a*), but become more circular by thickening round the edges, while rod-like synapticulæ divide each pore horizontally (Pl. IV, fig. 42, *a* and *b*). The breadth of the pore is the whole space between two septa. The septa themselves are so porous that the wall is a meshwork of rods rather than a porous lamina. A section through the wall thus shows a row of circular dots, some of which may be connected when the section has coincided with the rod-like portion of the wall between adjacent pores (Pl. IV, fig. 42). This is also indicated at *a* and *b*, fig. 38.

Another interesting feature is the occurrence of dissepiments in the central cavity near the base of the cup. In Pl. IV, figs. 39, 40, and 41, the ends of the septa are seen to cross the inner wall, and a certain amount of dissepimental tissue to be developed between them. Some of the longer outgrowths from the septa pass completely across the central space (figs. 40 and 41).

The discovery of the rooting processes in the above species is of interest, especially as these processes are not very unlike the cup in character, and it is possible that BORNEMANN had obtained some such similar forms, which he named

\* *Nova Acta der Ksl. Leop.-Carol. Deut. Akad. der Nat.*, vol. li, pp. 47, 48.

† *Mem. Roy. Soc. S. Australia*, vol. ii, part ii, 1910, p. 113.

*Protopharetra*, and then found that higher up a more regular type was attained. Another explanation of these processes may be suggested, namely, that they are really reproductive stolons which gave rise to new cups under favourable circumstances. This may or may not be the case, but they must have functioned in the fixation of the cup round which they occur.

It will be noticed that TAYLOR'S two new species of *Spiroclyathus* have been merged in the prototype, and the reasons for this will be seen by reference to the figures now published. The chief diagnostic characters in *S. irregularis*, as given by TAYLOR, are that the septa are much more radial near the inner wall and that they are very irregular towards the outer wall. This feature is beautifully shown in fig. 41, but, as stated already, fig. 40 is from the same specimen two sections below the level of fig. 41, and in the upper half of that figure (fig. 40) the septa are radial right out to the outer wall.

Again, Pl. III, fig. 32, and Pl. IV, fig. 37, are from the same specimen. In the former, radial symmetry is almost obliterated, but in the upper part of the latter figure this radial character of the septa is very prominent.

Similarly, *S. radiata*, Taylor, is merely a phase which occurs in places in each of the Weddell Sea forms. I have therefore placed them all under the prototype. VAN TOLL has figured a weathered specimen as *Spiroclyathus* sp., and his figure compares so well with that shown in Pl. IV, fig. 38, that this specimen is also included under *S. atlanticus*.

PROTOPHARETRA, Bornemann, 1883.\*

The most common type present in the *Scotia* material is undoubtedly referable to *Protopharetra*. BORNEMANN in his original description of the genus, considered it as a generalised type of basal structure from which many types might ultimately be developed, *i.e.* that different genera had similar basal structures. (An exact analogy has been shown in the fossil Lycopodiales, where *Stigmaria* includes the underground portions of *Lepidodendron*, *Sigillaria*, or *Bothrodendron*.) TAYLOR, while accepting BORNEMANN'S conclusion as far as the Sardinian forms are concerned, is emphatic in placing certain *completed* Australian types in the genus. Yet TAYLOR'S genus *Metaldetes* bears out BORNEMANN'S contention, since near the base a transverse section shows marked resemblances to *Protopharetra*. Both authors are probably correct, and the genus may be a central form which became differentiated along several lines.

*Protopharetra polymorpha*, Bornemann.

1884. *Protopharetra polymorpha*, Bornemann, *Geol. Zeitschr.*, p. 705.

1886. " " " " "Verstein. Sardinien," *Nova Acta der Ksl. Leop.-Carol. Deut. Akad. der Nat.*, vol. li, p. 46, Taf. v and vi.

A slightly oblique section (Pl. VI, fig. 66), which was obtained while making transverse sections from another specimen, compares very well as regards dimensions

\* *Geol. Zeitschr.*, 1883.

with one of BORNEMANN'S figured types (Taf. vi, figs. 3 and 4). The vertical character of the irregular septal plates is specially evident towards the base, where the section is more tangential. In transverse section the septa are seen to form an irregular meshwork (Pl. VI, fig. 65), which is crossed by delicate curved plates forming dissepimental tissue. The outer wall is well marked, as also is the inner. The septa are plates with irregular vertical corrugations which form a series of inosculating partitions between the two walls. Irregular emergences near the base appear to have fixed the whole cup (Pl. VI, fig. 66). A closer examination of the inner wall (fig. 65) shows that between the main septal plates small projections stretch into the intervallum, so that the inner wall becomes very conspicuous. In Pl. III, fig. 36, an enlarged view of the cup of Pl. VI, fig. 66, is given, and the inner wall is now seen to be porous. These pores (*p*) are small, probably 3 or 4 to the intersept, and this accounts for the presence, in transverse section, of the small structures between adjacent septa. They are really the divisions between the pores. But this figure illustrates another feature—the central cavity is filled by oblique cross partitions (*Boden* of BORNEMANN) between which numerous waved, vertical rods are clearly visible. Both the tabulæ and the rods are out-growths from the walls, and the whole completely fills in the central space. It would be difficult, however, to call this a coralloidal growth such as has been noted in *Thalamocyathus trachealis*, Taylor, sp.

*Protopharetra radiata*, Bornemann.

1886. *Protopharetra radiata*, Bornemann, "Verstein. Sardinien," *Nova Acta der Ksl. Leop.-Carol. Deut. Akad. der Nat.*, vol. li, p. 48, Taf. vii.

Several specimens of a rather larger form belong to this second species. The largest cup was 1 cm. in diameter, and indeed it was the largest complete cup obtained from the material. It is represented in Pl. III, fig. 35, and illustrates most of the features already described in *P. polymorpha*. The septa show a certain amount of thickening, and there is no sign of infilling material in the cup. Another specimen (Pl. VII, fig. 72) presents a good example of the branching in this species. The lowest section shows two cups joined together. Of these, one, *a*, has a clearly marked inner wall and the central cavity crossed by two tabulæ, while the ends of a few vertical rods are also visible. The central cavity of the second cup, *b*, is more completely filled, and consequently the inner wall is not so prominent. In the succeeding section (fig. 73) *a* has disappeared, *b* is cut at a higher level, and a third cup, *c*, with rooting process *r*, has joined itself to *b*. In the third section (fig. 74) *c* is cut at a higher level (very similar to that of *a*, fig. 72) and *b* has now disappeared. At *d* and *e*, however, sections of the presumed fixing strands are evident. The only distinction between *P. polymorpha* and *P. radiata* is one of size, the latter being larger in every way.

The question now arises, can we separate *Archæocyathus*, *Spirocyathus*, and *Protopharetra*? In the first place, it must be admitted that the greater number of species placed under the heading *Archæocyathus* are excluded at once from consideration, as they contain no dissepimental tissue, the structure which really causes all the complexity. It seems better to institute a new generic name for such simple forms, and the name *Thalamocyathus* has accordingly been adopted for such examples. In discussing the affinities of *Spirocyathus* and *Protopharetra* with *Archæocyathus*, the particular species one has in mind is *A. profundus*. That species is described more fully by HINDE than by BILLINGS. The outer and inner walls and septa are porous, the septa straight, and dissepiments oblique and imperforate. *Spirocyathus* has septa which are much corrugated, and the septal pores are large, a character also noticeable in *Protopharetra*. Dissepimental laminae are not nearly so common in *Spirocyathus* as in *Protopharetra*, and the inner wall is very distinctive, *Protopharetra* having several rows of pores between the septa, and *Spirocyathus* only one row.

Thus far *Protopharetra* has been considered as a distinct genus. We now pass to consider a similar type which gradually passes into quite a different form, and hence partly confirms BORNEMANN'S view that *Protopharetra* was a type of rooting structure rather than a genus complete in itself. Such examples are taken up under different generic names, and TAYLOR'S *Metaldetes* is a convenient genus for some types.

METALDETES, Taylor, 1910.\*

*Metaldetes plicatus*, sp. nov.

A type referable to TAYLOR'S genus *Metaldetes* is fairly common in small irregularly folded fragments. Complete examples seem rare, but one such is shown in Pl. VI, fig. 68. The cup has been distinctly plicated, and it is attached in part to a specimen of *Spirocyathus atlanticus*, which is seen in oblique longitudinal section near the top of the figure. There are certain well-marked characters in this new species. The septa are very numerous, straight and porous (as is indicated by the discontinuous course of the septa). The intervallum is very narrow, varying from 1 mm. to 1.3 mm., but where the section is oblique it seems much broader. Another distinct feature is the presence of numerous dissepiments, which, however, seem better described as irregular tabulae. They are much better displayed in longitudinal section (Pl. VI, fig. 69), and each crosses several loculi. The septa show here as vertical rods, again markedly discontinuous. These discontinuities are explained by reference to Pl. VI, fig. 71, *a* and *b*. Here an oblique longitudinal radial section of the cup crosses several septa, but the porous nature of these laminae is clearly indicated. The pores average 4 per mm.

\* *Mem. Roy. Soc. South Australia*, vol. ii, part ii, 1910.

The inner wall is also porous, as may be seen in Pl. VI, fig. 69, *w.p.*, but still more clearly in fig. 70 of the same plate. In size these wall pores are very similar to the septal pores, but the wall is not so well preserved as are the septa. The outer wall seems to be covered by a thin continuous lamina, but beneath this coating a porous structure similar to that on the inner wall may be noted in favourable sections. The dissepimental tissue is imperforate.

So far the specimens might quite well be placed in the genus *Archæocyathus*, but as they are cut at lower levels changes occur which place them quite outside that genus. In Pl. VII, fig. 75, there is shown what might be taken for a *Protopharetra* with closely set septal plates, and on the upper side, *a*, a small rooting process is attached. The next section is given in fig. 76, but now the septa are almost straight from wall to wall. Rooting processes are again shown, but the cup has become broken in outline. In fig. 77, from the section succeeding the last, the septa are still straighter; indeed, we now recognise the similarity to the cup of Pl. VI, fig. 68. At *a* of this figure a new cup is being formed from the wall of the old one, and it becomes more noticeable at *a*, fig. 78. Thus the form shown in Pl. VI, fig. 68, can be traced downwards into a rooting portion which is very similar to *Protopharetra*. This is precisely the character of TAYLOR'S genus *Metaldetes*. It will be readily admitted that the form of fig. 75 cannot be correlated with any of BORNEMANN'S species of *Protopharetra*, it is a much more delicate type than any he has described; but his contention that some forms of *Protopharetra* are the rooting or basal parts of other genera of the Archæocyathinæ is substantiated by the above series.

### Dictyocyathidæ.

DICTYOCYATHUS, Bornemann, 1891.\*

*Dictyocyathus*, sp. (Pl. VI, fig. 67.)

Among the small cups scattered through the material and only represented by a few sections is one shown in Pl. VI, fig. 67. There seem to be large pores on the inner wall, small ones on the outer wall, and very few septa joining the two walls. Too few sections have been cut to admit of a distinct specific description, but it constitutes a type quite different from any of the other forms obtained, and in all probability is referable to *Dictyocyathus*. The walls and transverse septal processes are thickened by subsequent layers of material, so that the outer wall becomes very thick at a level three or four sections below that figured. The only longitudinal section available shows the large pores of the inner wall; those on the outer wall are completely obliterated by the secondary growth.

\* "Verstein. Sardinien," *Nova Acta der Ksl. Leop.-Carol. Deut. Akad. der Nat.*, vol. lvi, 1891, pl. ii.

### Syringocnemidæ.

SYRINGOCNEMA, Taylor.\*

*Syringocnema gracilis*, sp. nov. (Pl. V, fig. 49; Pl. IV, figs. 43-48.)

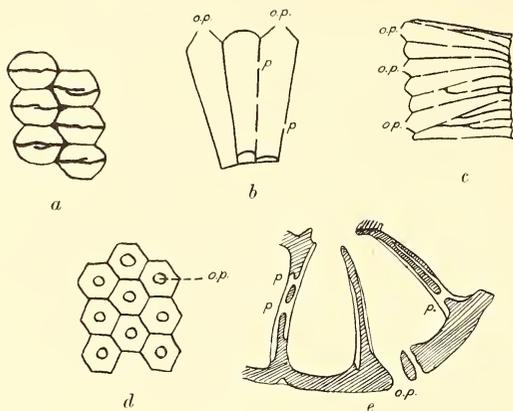
The genus *Syringocnema* was instituted for certain South Australian forms of the *Archæocyathinæ* which were very exceptional in structure. The outer and inner walls are not connected by septa, tabulæ, or dissepiments, but by a series of almost horizontal hexagonal tubes which had porous sides. Only one species was recorded, and no other form has since been discovered. Among the Weddell Sea material, however, four specimens were discovered which are indubitably referable to this genus. It happens that the preservation is not so good as in most of the other forms, but the essential characters can easily be demonstrated. The only rather unsatisfactory part is connected with the porous structure of the walls of the horizontal tubes.

A transverse section of the type (Pl. IV, fig. 43) is, at first sight, not unlike an ordinary *Archæocyathus*, but should the section be slightly oblique (Pl. IV, fig. 44) a very characteristic appearance is imparted to the whole cup. The apparent septa are seen to diverge and then converge in pairs. Where they diverge again from each other a cross wall joins them. The explanation of this phenomenon is given by oblique or tangential longitudinal sections (Pl. IV, fig. 47). Here the whole area of the section is covered by hexagonal cells, each being a section of one of the tubes which cross the intervallum. In longitudinal radial section it may be noted that the tubes are not absolutely horizontal, and that they bend down at their inner ends, and hence the apparent vesicular zone near the inner wall in some sections (Pl. IV, fig. 44, *α*).

Referring back to fig. 43, it will be noticed that the outer wall has not the regular outline usually seen in other *Archæocyathinæ*, but that each tube has a curved end convex outwards. In some cases (*p, p, p*) the end is more abrupt and projects further from the general line, so that an irregular toothed outline is imparted to the exterior. This again is best explained by longitudinal sections. In Pl. IV, fig. 45, such a section is shown. It is oblique, so that it cuts deeper into the tubes at the right-hand side, and is closer to the outer surface on the left. Proceeding from right to left across the figure, we notice progressive thickening of the walls of the tubes, and a consequent decrease in the lumen, until at the left-hand side the lumen is rounded instead of hexagonal, and the walls seem very thick. Now in transverse section (fig. 44) the walls are not much thickened, the apparent thickening being due to the contraction of the mouth of the tubes towards the exterior, so that the pore stands on the apex of a small conical projection from the general level of the wall (text-fig. 1 *b* and *c, o.p.*). The surface, if it could be exposed, would thus be covered by small papillæ, each with a pore on its apex. In *Syringocnema fавus*, Taylor, the

\* *Mem. Roy. Soc. South Australia*, vol. ii, part ii, 1910.

surface was minutely papillate, but the papillæ did not each correspond to a single intervallum tube. In one part of one of the specimens the outside lay on the exterior of the limestone, and a photograph is shown in Pl. V, fig. 49. The hexagonal character of sections of the tubes is well shown, but the level is too far below the actual surface to indicate the papillate character of the outer wall. The material was too limited to admit of sections being prepared to show the inner wall, etc.; but such sections as



TEXT-FIG. 1.

a, *Spiroclyathus atlanticus*.b, *Syringocnema gracilis*.c, *Syringocnema gracilis*.d, *do.*e, *Coscinoclyathus fultus*.

were made indicate that the inner wall is not papillate but smooth, and that the pores are the inner ends of the tubes.

The walls of the tubes are also porous, but the preservation is not very satisfactory. The best examples are in figs. 43 and 48, *v.p.* Here the pores are seen to be in two rows, and about 5 or 6 occur per mm. This character alone would differentiate *S. gracilis* from *S. fustus*, the only other known species which has three rows of pores on each wall and 3 pores per mm.

The main distinctions, however, lie in the very narrow intervallum in *S. gracilis*, from 1 to 1.4 mm., and in the narrow diameter of each tube, .4 to .5 mm. In *S. fustus* the corresponding dimensions are 5 to 6 mm. and 1 mm. respectively.

The vesicular zone near the inner wall is not so marked in *S. gracilis* as in *S. fustus*. In the latter type it is due to the great length of the tubes so that, where they bend down near the inner wall, several are cut through in any transverse section, and a broad, apparently vesicular zone formed.

Another interesting point shown by the new species is a coralloidal type of infilling towards the base of the cup, and an irregularity in the tubular arrangement. The new species may be defined as follows:—Cup conical; intervallum narrow (1 mm. to 1.5 mm.). Outer wall papillate, one pore on apex of each papilla. Pores lead into tubes (maximum diameter .5 mm.) hexagonal in section, lying horizontally between the walls. End of tube bent down near inner wall. Inner wall smooth, perforated, each pore the inner end of a separate tube. Apparent vesicles near inner wall due to sections of bent part of more than one tube. Vesicular zone of one row

only. Pores on tube walls in two rows, pores 5 or 6 per mm. Centre of cup filled near the base by coralloidal tissue. All skeletal structures sometimes thickened by secondary growth.

The specific name is due to the slender character of the walls and tubes.

### *Coscinocyathidæ.*

COSCINOCYATHUS, Bornemann, 1884.

The genus as described by BORNEMANN is characterised by the presence of horizontal tabulæ which mark it off from other forms of the group. The pores on the inner wall are defined as larger than those on the outer, but TAYLOR showed that this is not a constant feature. The Australian species described by the latter author have pores on both walls equal in size, and the Antarctic specimens conform to the Australian type rather than to the Sardinian. These Weddell Sea specimens fall into two categories, very distinct from one another and from all previously recorded *Coscinocyathidæ*. The mode of fixation of both types has been determined, and on this character alone they are easily distinguished.

#### *Coscinocyathus fultus*,\* n. sp.

Although only one complete specimen of this form and the tip of a second have been noted, the general character of the skeleton has been elucidated. The specimen from which most of the skeletal details have been obtained lay partially exposed on the side of the block. This weathered surface is illustrated by Pl. V, fig. 50, where the septa, the tabulæ (*t*), and porous inner wall (*i.w.*) are all obvious. The tabulæ at once place the form among the *Coscinocyathidæ*.

In transverse section most of the salient features become visible (Pl. VI, fig. 60). At *a* a small oval body, with its interior filled by convoluted partitions, is seen in close association with the main cup, and in a lower section, represented by fig. 61, several of these bodies are obviously connected to the surface of the cup. They become confluent round the periphery, and form a zone of vertical partitions surrounding the outer wall of the latter. Such offsets effect fixation of the whole structure. They occur in several series, and as new series are added the outer wall of the lower set is occluded, so that a series of walls, concentric with the outer wall of the cup, crosses the zone of vertical partitions (Pl. VI, fig. 60, *p*, *p*). These concentric walls are again seen in fig. 62, *p*, and it will be noticed that each reaches a higher level on the cup than does the one below. The vertical partitions are continuous across the concentric walls and are arranged perpendicularly to the latter.

The question as to the function of these bodies is more easily answered in this case than was possible in the case of *Spiroclyathus atlanticus*. As far as *Coscino-*

\* Lat. *fultus*, supported.

*cyathus fultus* is concerned, they appear to be organs of fixation, but they might also act as stolons, as was suggested in connection with similar strands in the former species. In *S. atlanticus*, however, there was no coalescence into exothecal lamellæ. It is interesting to note that such lamellæ have been recorded in two other forms, *Archæocyathus profundus*, Billings, and *A. Sellicksi*, Taylor. In neither of these cases has any confluence of small circular rooting structures been noted, but TAYLOR states that new cups may arise from the exothecal mass (*A. Sellicksi*), so that a certain amount of evidence exists pointing to the possibility that these processes function like stolons and produce new individuals.

Actual fixation has only been seen in one section, and this is shown in Pl. III, fig. 34. The cup is cut very close to the end, so that the central cavity *c* alone is obvious. The outer wall, *o.w.*, is also indicated, and round the whole are two layers concentric with the walls. Attached at one side is a process, *r.pr.*, which is fixed to a fragment of the cup of *Metaldetes plicatus* at *b*.

On account of the mass of enveloping lamellæ, and also since the walls and septa show considerable thickening, the details of the pores are difficult to determine. In longitudinal section (fig. 62) the pores of the outer wall are easily seen in several places, but the pore lumen is much reduced by thickening of the walls. The regularly placed tabulæ are also well marked in this figure (fig. 62, *t, t, t*). The pores run about 5 per mm. The porous structure of the inner wall is only shown on the weathered surface (Pl. V, fig. 50). There are two rows per intersept, and they number 5 per mm., as on the outer wall.

On account of the septal thickening, the porous structure on these elements has not been ascertained, although the pores are shown perforating the primary lamella (text-fig. 1 *e, p*). Tabulæ are shown in both figs. 60 and 61. They are very finely perforate; indeed, they might be described as net-like, since the pores are quite irregular in their distribution and closely pressed together. There are about 10 pores per mm. in any direction on the tabulæ.

Lastly, in the centre of the cup a mass of coralloidal tissue similar to that recorded by TAYLOR in *Somphocyathus* is very evident in Pl. VI, fig. 60. As noted earlier in this paper, similar coralloidal tissue has been discovered in *Archæocyathus trachealis* and *Syringocnema gracilis*, so that it can no longer be considered as an abnormality.

*Coscinocyathus endutus*,\* n.sp.

The second species of *Coscinocyathus* is represented by a considerable number of specimens cut in various directions, so that a more detailed examination has been possible. Like *C. fultus*, this form is quite dissimilar to any of the species so far recorded, the nearest being probably *C. irregularis*, Von Toll.

One of the chief diagnostic characters is the extraordinary mode of fixation.

\* *Gk. endutos*, clothed.

This will be clearly seen by reference to Pl. V, fig. 51, and Pl. III, fig. 33. The first of these figures represents the lowest transverse section of a cup which was obtained. The central cavity surrounded by six loculi occupies the centre. The walls separating the loculi are considerably thickened by callus growth. Surrounding the whole is a thick zone of lamellæ concentric with the cup, and presenting the appearance of an outer wall thickened by subsequent deposition of calcareous material. The latter figure, however, offers an explanation of the apparent thickening of the outer wall. Here the cup is cut longitudinally. Inner wall, septa, tabulæ, and outer wall are all shown, while at the base the whole vase-shaped organism is supported by a lamellar structure attached to a cluster of tubules of the alga *Epiphyton fasciculatum*, Chapman. The lamellæ then clothe the base of the cup in a close investment, the outer layers spreading at their base to give a firm support to the whole. But the lamellæ often spread laterally, embracing other remains and forming a pocket in which the base of the cup rests (Pl. V, fig. 52). In other cases groups of these plates attach themselves like struts to other organisms, expanding and flattening out on the supporting surface, and thus helping to steady the whole cup (Pl. V, fig. 53, *a*). As would be expected, the pores of the outer wall are obliterated where the investing laminae occur, but there being a sufficiency of material all the details of the porous structure were determined, as follows:—Pores on inner wall, 4 to 6 per mm.; on outer wall, 4 to 5 per mm.; on septa, 5 per mm.; on tabulæ (irregular meshwork rather than distinct pores), 8 or 9 per mm.

It will be noted in the above figures that there is considerable diversity in the size of pore, but I am averse to creating new species on pore size alone, for in two sections of the same specimen the measurements were 5 and 6 pores per mm. respectively. Nor do I consider the examples giving 4 pores per mm. sufficiently different in other respects to constitute a distinct species.

One of the best sections of the inner wall is shown in Pl. I, fig. 1, and has been already referred to. Here the pores run 4 per mm. A similar section from another specimen (Pl. V, fig. 53) shows pores 5.5 per mm. (In addition, the fixing lamellæ *a* are very conspicuous in this last figure.) The outer wall in the specimen of Pl. I, fig. 1, is figured in Pl. V, fig. 55, and again the pores run 4 per mm. As the inner pores and outer pores always correspond in size whether 4 per mm. or 6 per mm., the fossils are all of the "equivalium" type (TAYLOR).

The porous character of the septa is not so easily illustrated, but one good section is figured (Pl. V, fig. 57). When we consider the tabulæ the difficulty is greater, but in Pl. V, fig. 56, a small part of one of these is illustrated. The structure is an irregular meshwork rather than a regularly porous plate.

One of the figured sections (Pl. V, fig. 58) gives a good idea of the mode of new septal introduction, and also the irregular character of the tabulæ in many cases. While the new septa arise practically in whorls at the same level, yet that level does not seem to bear any relation to the tabulæ.

As in most of the other forms recorded, the interior of the cup becomes filled in towards the base by secondary structures. In the present instance this growth consists of irregular oblique tabulæ from which offsets pass in all directions. The resulting tissue is very spongy and completely fills the base of the cup. In Pl. V, fig. 53, the tissue is very evident. In Pl. V, fig. 58, it is again seen, though it does not form such a marked feature. In both these examples the fixing lamellæ are very distinct.

The perfectly longitudinal section of Pl. V, fig. 59, presents several interesting features. The fixing lamellæ are not well preserved at the base, though they are indicated, and become more obvious at a higher level (*l*). The tabulæ are quite irregular in distribution, and the central tissue is obviously developed from the inner ends of the tabulæ. The irregular offshoots from these tabular prolongations produce the coralloidal structure which is so marked in this figure.

This new species may be defined as follows:—

Cup small, vase-shaped. Fixed by lamellæ which wrap round the base and spread out over the substratum. Porous structure of outer and inner walls similar (equivalum type); pores 4-6 per mm. Septa regular, perforate (5 pores per mm.); tabulæ irregular, a meshwork rather than a porous platform; mesh 8 or 9 per mm. Base of cup filled by coralloidal growth, the result of proliferations from the tabulæ into the central space.

#### SUMMARY.

The organic remains represented in two small pieces of limestone dredged from a depth of 1775 fathoms in lat. 62° 10' S., long. 41° 20' W., are described.

These consist of both plant and animal fragments and skeletons. The plants are calcareous algæ and may be referred to the genus *Epiphyton*, Bornemann.

The animal remains are spicules, probably from sponges, complete and fragmentary cups of Archæocyathinæ, and sections of the carapace of trilobites.

The sponge spicules may be referred to the groups Tetractinellida, Hexactinellida, and Heteractinellida. A peculiar forked type is also represented, but it is quite unlike the modern *Lelapia* in structure.

The Archæocyathinæ belong to a number of different genera. Some of the species have been recorded from other parts of the world, but some are new forms. In certain of the known types, new structures have been recorded, and a more accurate specific description than was formerly given has thus been made possible.

TAYLOR'S grouping of the family Archæocyathidæ has been revised and a new genus (*Thalamocyathus*) instituted. *Thalamocyathus* contains groups I to IV of *Archæocyathus* as defined by that author. Thus in the Archæocyathidæ are included *Archæocyathus*, *Thalamocyathus*, *Ethemophyllum*, *Archæofungia*, and *Pycnidocyathus*.

## CONCLUSIONS.

At the outset it must be admitted that this research has not led to any more definite ideas regarding the type of organism which secreted the *Archæocyathus* forms of skeleton. The method of cutting sections in definite directions has allowed, however, of a more minute description of certain skeletal types. In several forms the means of fixation of the skeleton have been determined, and these are not constant for all species of the same genus, while closely similar methods of fixation occur in different genera. Thus *Spiroclyathus atlanticus* and *Coscinocyathus fultus* have root-like emergences acting as stout supports (perhaps also as stolons), while *Coscinocyathus fultus* and *C. endutus* have very different methods of fixation.

It is suggested that the fixing strands may have functioned as stolons producing a vegetative increase in the number of individuals, but no case has been seen where new cups actually arise from these emergences. TAYLOR, however, records a cup arising from exothecal lamellæ (fixation lamellæ) in *Archæocyathus Sellicksi*,\* though even there it is not clear whether the new cup arose from the exothecal structures or was merely fixed to them. Apart from the fixation structures, there are one or two marked features in this fauna from Antarctic regions. In the first place, the specimens are small; secondly, they show, in the majority of cases, marked thickening of the walls near the base; and thirdly, there are a great number of specimens (and these belong to different genera and species) in a very small amount of material, *i.e.* the fauna was abundant and varied, but the individuals small in size. The largest example is under 30 mm. long, and the greatest diameter noted in any cup is 10 mm. or thereby. This compares very unfavourably with specimens from any recorded locality, save only the other Antarctic record, from 85° S. on the Beardmore Glacier. Despite the small size, the skeletal characteristics are constant and quite comparable with similar forms from other regions.

Thickening of the walls and septa occurs near the base in several species, and this is accompanied by a partial filling of the central cavity by ingrowths from the inner wall. Such infilling may be an irregular coralloidal mass (*Thalamocyathus trachealis*, *Coscinocyathus fultus*, etc.) or a series of twisted tabulæ (continuations of similar structures crossing the intervallum), with the interspaces filled by more irregular tissue (*Protopharetra polymorpha*, Pl. III, fig. 36). Both of these characters seem best regarded as gerontic features, or as indicating that the specimens were at any rate mature. In either case, when combined with the small size of the specimens, they point to the conclusion that the conditions under which the organisms lived were far from favourable to their growth, maturity supervening while the organism was small; or, what amounts to the same, growth being exceedingly slow. Such a conclusion is confirmed rather than refuted by the fact that so many varied types occur in a very small volume of material. It has been pointed out in various records that great

\* *Mem. Roy. Soc. S. Australia*, vol. ii, part ii, 1910, text-fig. 9.

abundance of certain forms in one bed or horizon (especially when the forms are small) does not necessarily indicate that the conditions then obtaining were favourable for that particular organism. More commonly it indicates quite the reverse, for the small size is frequently accompanied by gerontic characters showing that the growth was very slow, *i.e.* that the forms were stunted in their development.

Since all the specimens were small and relatively complete, the early stages of growth were obtained in practically all cases. Thus in particular it was possible to test the truth of BORNEMANN'S idea that *Protopharetra* is not a genus of the Archæocyathinæ, but represents a general type of rooting structure, *i.e.* that various genera may terminate downwards in *Protopharetra* forms. (A direct analogy may be seen in the so-called genus of plants—*Stigmaria*—which has been proved to be a general type of rooting structure common to *Lepidodendron*, *Sigillaria*, and *Bothrodendron*.) TAYLOR'S genus *Metaldetes* certainly lends colour to BORNEMANN'S view, and so also does *Spirocyathus*, as shown above; but, in spite of the fact that a casual examination might cause one to group the lower parts of the skeletal remains with *Protopharetra*, a closer examination shows that there are differences, and that *Protopharetra* is a distinct genus.

The biological position of the whole group is still doubtful. The porous skeleton suggests affinities with the Porifera, though not necessarily so, since certain of the Cœlenterata also have porous walls. The non-spicular character of the walls, septa, etc., and the thickening of these structures in the lower parts of the cup, favour relationships with corals (Anthozoa), while the peculiar internal growths can also be paralleled in that group. The points of difference, on the other hand, are too conspicuous to allow of any such correlation. Indeed, it is quite as likely that the resemblances to sponges and corals are merely superficial and can be explained as homoplastic developments.

Nor can we point to any gradual evolutionary changes within the group itself which might give some clue to possible lines of descent. The Archæocyathinæ appear suddenly as a suite of very diverse forms at the top of the Lower Cambrian Series, and on that geological horizon have practically a world-wide distribution. True, a supposed organism, *Atikokania*, Walcott, from Pre-Cambrian rocks was compared with the Archæocyathinæ, but the author has since proved that the structure was really produced by inorganic means. The whole group, therefore, is very isolated and has an extremely short geological range.

There is certainly abundant evidence that sponges coexisted with these organisms, but corals are conspicuously absent from rocks of this period. Yet it must be borne in mind that many Cœlenterata secrete no skeletal elements, so the absence of anthozoan skeletons from Lower Cambrian rocks does not necessarily imply that the class was not represented in the fauna of that age. The only fossil with any marked similarity to the Archæocyathinæ is the calcareous sponge *Barroisia* from Cretaceous rocks. Here, however, the skeleton is spicular and its sponge characters undoubted.

In the Archæocyathinæ we are thus confronted with a large, diverse, and widely spread fauna, which appears suddenly at an early stage of the organic history of the world, which produced locally great reefs of calcareous material in the oceans of that date, and which became extinct as suddenly as it had appeared.

Having merely a series of skeletons to work from, comparison can only be made with skeletons exhibiting similar shape and structure, and, despite the non-spicular nature of the skeleton, it seems more natural to group these organisms with sponges than with any other class of the animal kingdom. Of course it may be argued that the characters justify the creation of a new phylum, though, at present, such a course does not seem necessary.

While the salient points in the anatomy of the skeleton in most species are clear, the nomenclature of the group is far from satisfactory. It is impossible to group the present forms known as *Archæocyathus* under BILLINGS' original or emended definition. TAYLOR has given a subdivision of the genus *Archæocyathus*, but several of his divisions are quite worthy of generic rank. The only forms which can be included in the genus as defined by BILLINGS are *A. profundus*, Billings, *A. Sellicksi*, Taylor, *A. dissepimentalis*, Taylor, and *A. pauciseptatus* described above. All the other species given under this generic title have no dissepimental tissue, and it seems as logical to place them in some new genus as to place those which have tabulæ in the genus *Coscinocyathus*. It may be objected that in one case (*A. Sellicksi*) the dissepiments only occur near the base, and that it is really intermediate between the two types at present grouped under the name *Archæocyathus*. But there are connecting forms between other genera, and it seems preferable to keep BILLINGS' definition for *Archæocyathus* and erect a new genus to contain those forms which have straight septa and neither dissepiments nor tabulæ.

For this reason the genus *Thalamocyathus*, as defined above, has been instituted. Forms, therefore, with straight septa and neither tabulæ nor dissepiments come into the genus *Thalamocyathus*; those which have straight septa and well-marked tabulæ are grouped under the name *Coscinocyathus*; specimens with straight septa but irregular tabulæ and dissepiments remain in the original genus of BILLINGS, *Archæocyathus*.

In considering this flora and fauna from a geological point of view, it will be convenient to summarise the whole as follows:—

#### FLORA.

##### *Algæ.*

*Epiphyton fasciculatum*, Chapman.

„ *grande*, sp. nov.

#### FAUNA.

##### *Porifera.*

*Tetractinellida*, *Hexactinellida*, *Heteractinellida*.

*Archæocyathinæ.*

- Archæocyathus pauciseptatus*, sp. nov.  
*Thalamocyathus flexuosus*, sp. nov.  
 ,, *ichnusa*, Meneghini, sp.  
 ,, *infundibulum*, Bornemann, sp.  
 ,, *trachealis*, Taylor, sp.  
 ,, *tuberculatum*, Taylor, sp.  
*Spirocyathus atlanticus*, Billings, sp.  
*Syringonema gracilis*, sp. nov.  
*Coscinoocyathus endutus*, sp. nov.  
 ,, *fulvus*, sp. nov.  
*Protopharetra polymorpha*, Bornemann.  
 ,, *radiata*, Bornemann.  
*Metaldeles plicatus*, sp. nov.  
*Dietyocyathus* sp.

The presence of algæ in this limestone at once imposes certain limits to the depth at which the rock must have been formed, for these plants could not have lived in the complete absence of light. At the same time, the rock consists entirely of calcareous material without admixture of sand grains. The deposit, then, must have formed in shallow, clear water, possibly with little or no current action.

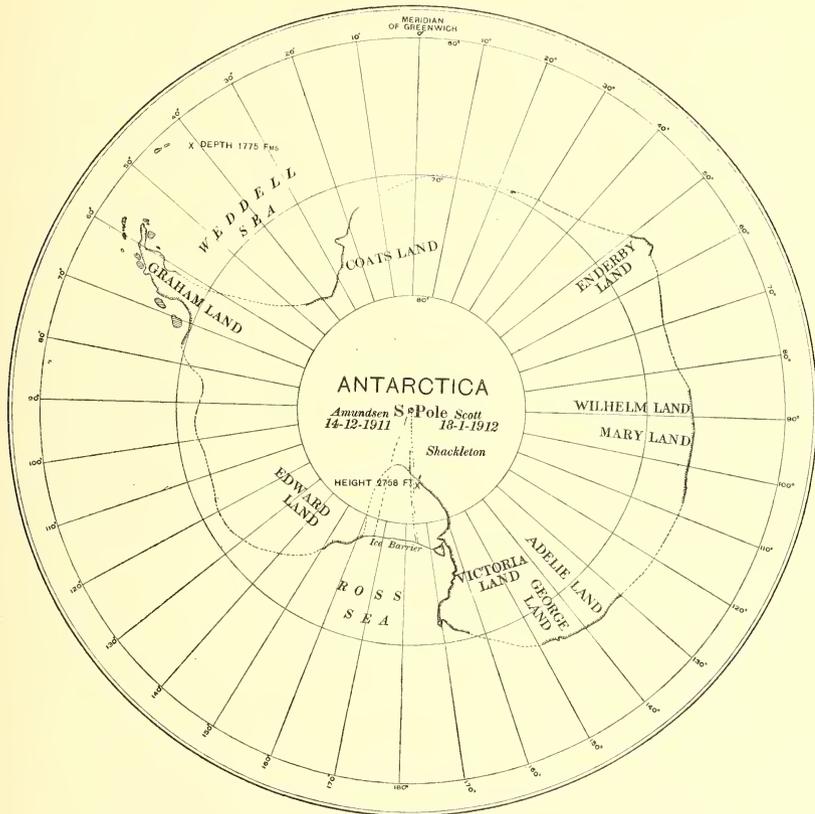
In comparing the above list of organic remains with similar lists from other areas, it is natural to consider, in the first place, Antarctic localities. In the various reports of the British Antarctic Expedition, records of a Cambrian flora and fauna are given, but unfortunately the material obtained was not very perfect. TAYLOR'S report\* states that two families of the Archæocyathinæ were certainly present, namely, the Archæocyathidæ and Spirocyathidæ. CHAPMAN † describes the alga *Epiphyton fasciculatum* from the same area, and, although the material seems badly preserved and consequently his figures rather defective, there is no doubt that one of the algæ recorded above is identical with his species. Another fossil common to the two localities is the forked sponge spicule which TAYLOR has compared with *Lelapia*. Several of these forked forms have been noted in Weddell Sea material, and the evidence now available shows that the spicule was probably a hexactinellid type in which one ray is branched. So far, then, as the record from the Beardmore Glacier goes, it shows a wonderful similarity with the Weddell Sea record. These localities ‡ are approximately on opposite sides of the South Pole (text-fig. 2, X, X'), but in neither case has the material been obtained *in situ*.

\* *British Antarctic Expedition*, 1907-9, "Geology," vol. i, p. 240.

† *Ibid.*, vol. ii, pp. 81-83.

‡ Bruce, Weddell Sea position, 62° 10' S., 41° 20' W., Scottish National Antarctic Expedition, 1902-4; Shackleton, Beardmore Glacier position, 83° 42' S., 171° 30' E., British Antarctic Expedition, 1907-9, "Geology," vol. i, p. 235.

The drift in both cases has apparently been more or less northwards, but it is impossible to assign any southern limit to the localities from which they may severally have been drifted. All one can say is that somewhere in Antarctica there



TEXT-FIG. 2.

must have been a development during Cambrian times of limestone containing *Archæocyathinæ* and marine algæ.

A much more useful comparison, however, may be made with the Cambrian fauna of South Australia. As described by TAYLOR, it constitutes the most complete and most extensive *Archæocyathus* fauna yet recorded.

The following genera are represented:—

Archæocyathus.	Ethmophyllum.
Thalamocyathus.	Metaldetes.
Archæofungia.	Protopharetra
Archæosyon.	Pycnoidocyathus
Coscinoocyathus.	Spirocyathus.
Coscinoptycha.	Somphocyathus.
Dietyocyathus.	Syringocnema.
Dokidocyathus.	

It will be noted that all the genera from the Weddell Sea material are represented in South Australia, and that two of these (*Metaldetes* and *Syringocnema*) have not been obtained elsewhere.

While the majority of the species in the two areas are distinct, yet some forms are common to both faunas, and one of the species, viz. *Thalamocyathus trachealis* (Taylor, sp.), is confined to these two localities. Even among the forms which are not specifically identical there are sometimes similar characteristics. For example, the species of *Coscinoocyathus* from South Australia have, in the majority of cases, the pores on the inner wall equal in size to those on the outer wall, i.e. they are of the "equivalum" type. In other records the *Coscinoocyathidæ* have larger pores on the inner wall. The Antarctic examples described above approximate to the Australian "equivalum" type.

All these cases point to a close relationship between the Antarctic and Australian faunas of Lower Cambrian age; and comparison with the *Archæocyathus* fauna in Sardinia, Canada, or Siberia shows that the forms are not nearly so closely allied. There is, however, one marked point of contrast, namely, the size and general condition of the specimens. TAYLOR has recorded specimens from Australia reaching a length of 6 inches and a diameter of 4 inches. The longest example from the Weddell Sea is little more than 1 inch, and the greatest diameter recorded is about  $\frac{2}{3}$  inch. Again, as shown above, the walls and septa are in most cases thickened, while the interior of the cup is filled with adventitious structures. These features are considered gerontic. The small size and apparently senile characters mark the Weddell Sea types and probably indicate life under adverse circumstances. It is interesting to note that the only complete specimens recorded from the Beardmore Glacier moraines were embryonic forms, according to TAYLOR. This is explained in the Report of the British Antarctic Expedition as due to the small size of the fragments of the breccia; but none of the fragments of larger cups—as far as one can judge—indicate very large individuals. The small size may again be explained by adverse conditions of growth, and in that case can be correlated with the Weddell Sea forms.

Taking all these facts into consideration, we seem driven to the conclusion that the life-types of Cambrian times in South Polar and Australian areas were similar, but that conditions towards the pole were less favourable for the growth of these

organisms. The most obvious way in which the conditions could be adverse is by a climatic change, since other characters seem similar. It will be interesting to see whether subsequent discoveries confirm an apparent climatic differentiation during Cambrian times.

In conclusion, I desire to record my thanks to Dr W. S. BRUCE, leader of the *Scotia* Antarctic Expedition, for giving me the opportunity of examining and describing the Weddell Sea specimens, and for his forbearing in the long delay in publication; to Professor W. W. WATTS, F.R.S., who has acted as supervisor, for the University of London, and read over the manuscript; and to Professor J. H. ASHWORTH, F.R.S., who, in my absence, read the paper to the Society. I am also indebted for assistance in preparing the sections of the material to Mr C. H. BENSON; to Mr J. MATHESON, who has constructed the map showing the geographical points of Antarctica referred to in the text; and to the Carnegie Trust for the Universities of Scotland for a generous grant to defray the cost of publication.

#### EXPLANATION OF PLATES.

(All figures are prints from untouched negatives.)

#### PLATE I.

Fig. 1. *Coscinocyathus endutus*. Longitudinal section through inner wall. *a*, inner wall present; *b*, inner wall replaced by crystalline calcite, porous structure indicated by darker matrix; *c*, pores on outer wall. (Slide S. 97,  $\times 7.5$ .)

Fig. 2. *C. endutus*. External surface of weathered specimen. Outer wall practically all removed by weathering. Porous structure still indicated near the base and on the sides. Septa and tabulæ also shown as a series of cavities arranged in lines. *a*, septum, the holes really represent the solid part of the original septum, which is here dissolved away, while the solid part between the holes is the matrix filling in an original pore; *b*, tabulæ. (Slide S. 156,  $\times 5$ .)

Fig. 3. *Epiphyton fasciculatum* and *E. grande*. The relative sizes of the tubules are quite easily seen. *a*, *E. fasciculatum*; *b*, *E. grande*. (Slide S. 44,  $\times 9$ .)

Fig. 4. *E. fasciculatum*. Slightly enlarged view of the thallus to show the tufted character. *a*, portion more highly magnified in fig. 4a. (Slide S. 69,  $\times 25$ .)

Fig. 4a. *E. fasciculatum*. Portion of *a* (fig. 4) more highly magnified to illustrate the equal bifurcations of the thallus and the swollen terminal portions. *a*, points of bifurcation. (Slide S. 69,  $\times 90$ .)

Fig. 5. *E. grande*. General view of a large tuft cut obliquely. Bifurcating character very apparent in places. (Slide S. 11,  $\times 25$ .)

Fig. 6. Sponge spicule; probably heteractinellid. (Slide S. 103,  $\times 20$ .)

Fig. 7. Sponge spicule; tetractinellid type, showing all four rays. (Slide S. 33c,  $\times 20$ .)

Fig. 8. Sponge spicule; large form, probably heteractinellid. (Slide S. 113,  $\times 20$ .)

Fig. 9. Spicule similar in type to that of fig. 8. (Slide S. 81,  $\times 20$ .)

Fig. 10. Sponge spicule; hexactinellid form. (Slide S. 23,  $\times 20$ .)

Fig. 11. Sponge spicule; tetractinellid. Three rays beautifully displayed; the fourth is vertical, but is indicated by the knob at *a*. (Slide S. 76,  $\times 20$ .)

Fig. 12. Sponge spicule. Hexactinellid type with one ray bifurcated. Similar to *Lelapia*-like spicule of TAYLOR. *a*, spicule cut through median plane; *b*, a second example showing bifurcated ray only, as section is oblique to median plane. (Slide S. 102,  $\times 90$ .)

Fig. 13. Another spicule similar to that of fig. 12, but cut rather obliquely. (Slide S. 78,  $\times 90$ .)

- Fig. 14. Hexactinellid spicule of ordinary type. (Slide S. 36c,  $\times 20$ )  
 Fig. 15. *Thalamocyathus tubavalium*. Transverse section of cup. *a, b*, stirrup-pores. (Slide S. 125,  $\times 10$ .)  
 Fig. 16. *Epiphyton fasciculatum*. Transverse section through thallus, showing numerous tubules filled by a matrix of granular calcite. (Slide S. 140,  $\times 26$ .)

## PLATE II.

*Thalamocyathus trachealis*, Taylor, sp.

- Fig. 17. Transverse section of young cup, showing a considerable number of septa but no infilling by callus growth into the central cavity. (Slide S. 88,  $\times 28$ .)  
 Fig. 18. Transverse section of largest specimen obtained. *a, a*, pores on outer wall. (Slide S. 4,  $\times 5.5$ .)  
 Fig. 19. Transverse section of cup, shown in last figure, at a lower level. Internal ring-platforms prominent. Fringe of peg-like outgrowths from lower surface of shelf at *a*. See Pl. III, fig. 26. (Slide S. 22,  $\times 22$ .)  
 Fig. 20. Transverse section of cup to show a complete ring-platform. At *a* the platform is complete, at *b* only the outer rim is indicated. Septal pores at *c*. (Slide S. 23,  $\times 22$ .)  
 Fig. 21. Longitudinal section of outer wall to illustrate the porous structure. (Slide S. 18,  $\times 21$ .)  
 Fig. 22. Longitudinal section of inner wall. *a*, pores; *b*, ring-platform cut vertically; *d*, septa; *c*, peg-like denticles on lower surface of platform. (Slide S. 14,  $\times 21$ .)  
 Fig. 23. Longitudinal section to show septal pores. *a*, pores on outer wall; *b*, peg-like projection from under side of ring-platform; *c*, septum with pores. (Slide S. 15,  $\times 22$ .)  
 Fig. 24. Longitudinal section of Australian specimen from Ajax Hill, Beltana, South Australia. *a*, pores on outer wall; *b*, peg-like projections on lower side of ring-platform; *c*, septum with pores. (Slide S. 161,  $\times 22$ .)  
 Fig. 25. Transverse section of a specimen showing coralloidal structures filling in the central cavity. (Slide S. 26,  $\times 7.5$ .)

## PLATE III.

- Fig. 26. *Thalamocyathus trachealis*. Transverse section of cup, part *a* of Pl. II, fig. 19, highly magnified to show the row of peg-like projections. *s*, septum; *p*, septal pore; *a*, row of pegs in action. (Slide S. 22,  $\times 90$ .)  
 Fig. 27. *T. flexuosus*. Transverse section of fragment of large cup. (Slide S. 47,  $\times 3$ .)  
 Fig. 28. Longitudinal section of inner wall of *T. flexuosus*. Stirrup-pores indicated at *b*. (Slide S. 46,  $\times 9$ .)  
 Fig. 29. *T. flexuosus*. Longitudinal section of outer wall. *s*, septa indicated between pore rows, *i.e.* no stirrup-pores. (Slide S. 45,  $\times 9$ .)  
 Fig. 30. *T. infundibulum*. Longitudinal section through inner wall. (Slide S. 91,  $\times 10$ .)  
 Fig. 31. *T. ichnuse*. Oblique longitudinal section showing pores on inner wall and septa. (Slide S. 58,  $\times 10$ .)  
 Fig. 32. *Spirocyathus atlanticus*. Transverse section of cup. (Slide S. 35c,  $\times 11$ .)  
 Fig. 33. *Coscinoocyathus endatus*. Longitudinal section of young cup. *i.w.*, inner wall with pores; *o.w.*, outer wall; *s*, septum with pores; *t*, tabula. (Slide S. 29,  $\times 26$ .)  
 Fig. 34. *C. fultus*. Oblique section of young cup showing fixing process (*r.pr.*). *b*, base on which the cup is fixed (it is part of a cup of *Metalldetes plicatus*); *o.w.*, outer wall much thickened; *c*, central cavity.  
 Fig. 35. *Protopharetra radiata*. Complete transverse section of largest cup obtained. (Slide S. 29,  $\times 9$ .)  
 Fig. 36. *P. polymorpha*. Longitudinal section of central cavity. The complete specimen is figured at Pl. VI, fig. 66. Cavity filled in by proliferations from inner wall and disseptimental tissue. *p*, pores on inner wall. (Slide S. 2,  $\times 10$ .)

## PLATE IV.

- Fig. 37. *Spirocyathus atlanticus*. Transverse section of cup near top. (Slide S. 37,  $\times 9$ .)  
 Fig. 38. *S. atlanticus*. Oblique section showing that the septa are more like a meshwork of rods than a plate perforated by pores, and thus accounting for the disconnected type of septum as seen in transverse section. (Slide S. 48,  $\times 2.5$ .)

Fig. 39. *S. atlanticus*. Transverse section at a low level, with rooting processes (*a, b, c*) surrounding the cup. (Slide S. 33*a* (2),  $\times 9$ .)

Fig. 40. *S. atlanticus*. Transverse section of cup at a higher level than in last figure. *a*, rooting process attached to the cup. (Slide S. 35*a* (2),  $\times 9$ .)

Fig. 41. *S. atlanticus*. Transverse section of same cup as figured in last two photographs, but cut at a still higher level. (Slide S. 36*a*,  $\times 9$ .)

Fig. 42. *S. atlanticus*. Longitudinal section of cup to show pores on inner wall and septa. *a* and *b*, pores on inner wall. See also text-fig. 1*a*. (Slide S. 41,  $\times 9$ .)

Fig. 43. *Syringocnema gracilis*. Transverse section of small cup. *p, p, p*, pores on pyramidal papillae of outer wall; *w.p.*, pores on wall of tube. See also text-figs. 1*b, 1c*, and 1*d*. (Slide S. 112,  $\times 12$ .)

Fig. 44. *S. gracilis*. Transverse section of fragment of large cup. *a*, apparent vesicular tissue near inner wall due to the inner ends of the tubules bending downwards. See text-fig. 1*c*. (Slide S. 118,  $\times 10$ .)

Fig. 45. Longitudinal section near outer wall. On the left the pores on outer wall are visible; on the right the tubules are cut further in towards the interior, and thus appear wider in the lumen. (Slide S. 120,  $\times 10$ .)

Fig. 46. *S. gracilis*. Oblique longitudinal section of small cup. *a*, tubules in longitudinal section. (Slide S. 112,  $\times 10$ .)

Fig. 47. *S. gracilis*. Tangential section through tubules. Section from same specimen as fig. 44, but cut perpendicular to the direction of the latter. (Slide S. 121,  $\times 10$ .)

Fig. 48. *S. gracilis*. Transverse section near the base of small cup. Interior filled by coralloidal growth. *w.p.*, pores on walls of tubules. (Slide S. 108,  $\times 10$ .)

## PLATE V.

Fig. 49. *Syringocnema gracilis*. Weathered surface showing tubules in section. (Slide S. 115,  $\times 8$ .)

Fig. 50. *Coscinocyathus fultus*. Weathered surface on outside of block. This specimen was cut up into sections in various directions and the surface therefore destroyed. *t*, tabulae; *i.w.*, inner wall with pores.  $\times 5$ .

Fig. 51. *C. endutus*. Transverse section near apex of cup. The characteristic investing lamellae are very well developed. Septa at this level six in number. (Slide S. 31*a*,  $\times 26$ .)

Fig. 52. *C. endutus*. Section at a slightly higher level. The investing lamellae are spreading out and anchoring the cup to surrounding objects. (Slide S. 66,  $\times 9$ .)

Fig. 53. *C. endutus*. Section above that of fig. 52. It becomes oblique at the top, and the pores of the inner and outer walls are visible. *a*, bundle of fixation-lamellae. Interior of cup filled by coralloidal growth. (Slide S. 67,  $\times 9$ .)

Fig. 54. *C. endutus*. Oblique longitudinal section of outer wall. The wall has disappeared, but the porous character is preserved by the dark matrix. See also Pl. I, fig. 1. (Slide S. 55,  $\times 9$ .)

Fig. 55. *C. endutus*. Longitudinal section of outer wall to show porous character. (Slide S. 98,  $\times 9$ .)

Fig. 56. *C. endutus*. Transverse section through septum illustrating the irregular perforations; from same specimen as shown in Pl. I, fig. 1. (Slide S. 99,  $\times 28$ .)

Fig. 57. *C. endutus*. Longitudinal section through a septum to show the pores. (Slide S. 27,  $\times 9$ .)

Fig. 58. *C. endutus*. Oblique longitudinal section through cup. Irregular spacing and course of septa well shown. *l*, fixation-lamellae; *a*, transverse section of cup of *Protophætra polymorpha*. (Slide S. 53,  $\times 5.5$ .)

Fig. 59. *C. endutus*. Longitudinal section through cup. The internal coralloidal tissue is particularly well exhibited. *l*, fixation-lamellae. (Slide S. 53,  $\times 10$ .)

## PLATE VI.

Fig. 60. *Coscinocyathus fultus*. Transverse section of cup. *a, b*, rooting processes; *p, p*, external boundaries of successive series of fixation offsets; *t*, tabula; *c.t.*, coralloidal tissue in central cavity. (Slide S. 153,  $\times 9$ .)

Fig. 61. *C. fultus*. Section below that of last figure. *a, c*, rooting processes; *p*, boundary between two of these processes; *t*, tabula. (Slide S. 152,  $\times 9$ .)

Fig. 62. *C. fultus*. Longitudinal section of outer wall. The porous structure of the latter is prominent in places. *p, p*, boundaries between rooting offsets; *t*, tabula. (Slide S. 154,  $\times 9$ .)

Fig. 63. *Archaeocyathus pauciseptatus*. Transverse section of cup. At *p* the septa are seen to be porous. (Slide S. 145,  $\times 9$ .)

Fig. 64. *A. pauciseptatus*. Longitudinal section. Imperforate outer lamina is clearly seen on each side. *p*, septal pore; *i.w.*, porous inner wall; *c.t.*, coralloidal tissue in central cavity. (Slide S. 148,  $\times 9$ .)

Fig. 65. *Protopharetra polymorpha*. Transverse section of cup. (Slide S. 33a (1),  $\times 9$ .)

Fig. 66. *P. polymorpha*. Longitudinal section. Central portion at *d* is shown in Pl. III, fig. 36. (Slide S. 2,  $\times 3.5$ .)

Fig. 67. *Dictyocyathus* sp. Transverse section illustrating very irregular rod-like septa. (Slide S. 54,  $\times 11$ .)

Fig. 68. *Metaldetes plicatus*. Transverse section through rather irregular cup which is attached to a portion of *Spirocyathus atlanticus* along the top. (Slide S. 49,  $\times 3$ .)

Fig. 69. *M. plicatus*. Longitudinal section showing septa, which are porous, crossed by a very irregular set of curving tabulae. *w.p.*, pores on outer wall. (Slide S. 90,  $\times 9$ .)

Fig. 70. *M. plicatus*. More highly magnified figure of pores on outer wall, shown as *w.p.* in last figure. (Slide S. 90,  $\times 27$ .)

Fig. 71. *M. plicatus*. Longitudinal section of a septum to illustrate the porous character. *a, b*, septum with pores. (Slide S. 94,  $\times 9$ .)

#### PLATE VII.

Fig. 72. *Protopharetra radiata*. Transverse section near point of bifurcation of a cup. *a*, one cup cut near the top, inner wall developed and little tissue in central cavity; *b*, cup cut lower down than in *a*. Inner wall not so clearly visible, and centre filled in by coralloidal growths. (Slide S. 65,  $\times 5$ .)

Fig. 73. *P. radiata*. Transverse section above that of fig. 72. The section passes above the level of cup *a*; *b* is cut at a higher level than in the last figure, and a third cup *c*, with rooting processes *r*, is now joined to *b*. (Slide S. 66,  $\times 5$ .)

Fig. 74. *P. radiata*. Transverse section above level of fig. 73. The cup *b* has now disappeared, while *c*, with its rooting offsets *d* and *e*, has reached a level where the inner cavity is nearly free from infilling material and thus the inner wall is prominent. (Slide S. 67,  $\times 5$ .)

Fig. 75. *Metaldetes plicatus*. Transverse section at a low level. *a*, rooting process. (Slide S. 52,  $\times 9$ .)

Fig. 76. *M. plicatus*. Section of the same cup at a higher level. (Slide S. 53,  $\times 9$ .)

Fig. 77. *M. plicatus*. Section above that of fig. 76. *Metaldetes* form now well developed. *a*, new cup forming from the wall of the older cup. (Slide S. 54,  $\times 9$ .)

Fig. 78. *M. plicatus*. Topmost section of cup. *a*, the new cup at a higher level than in last figure, and having the *Protopharetra* form of the early stage (fig. 75) of the present cup. (Slide S. 55,  $\times 9$ .)

Dr W. T. GORDON: "Cambrian Organic Remains from Weddell Sea."—PLATE I.



FIG. 1.



FIG. 6.



FIG. 7.



FIG. 8.



FIG. 2



FIG. 9.

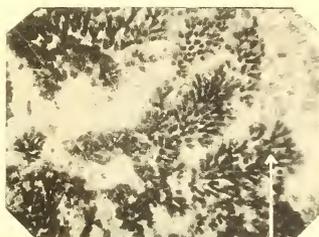


FIG. 4.



FIG. 10.



FIG. 3.



FIG. 11.



FIG. 14.

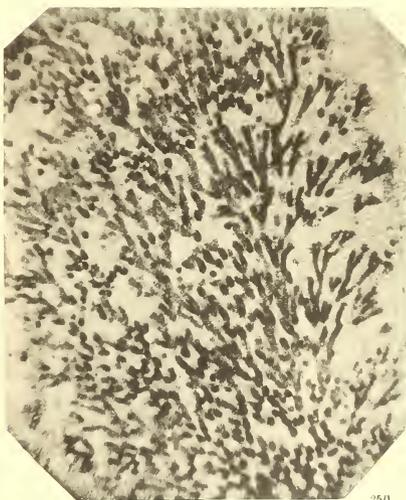


FIG. 5.

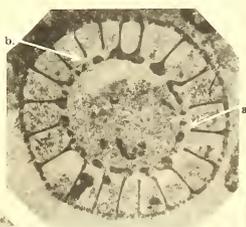


FIG. 15.

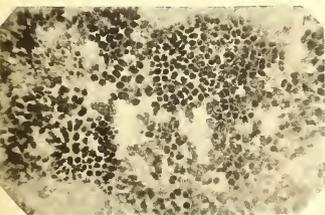


FIG. 16.



FIG. 13.

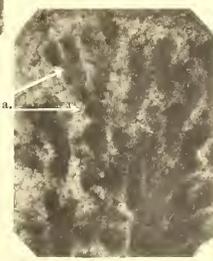


FIG. 4A.



FIG. 12.



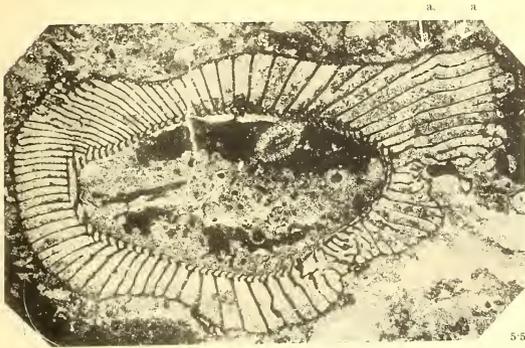


FIG. 18.

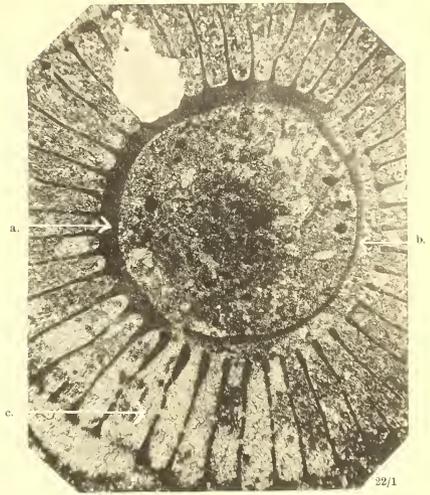


FIG. 20.

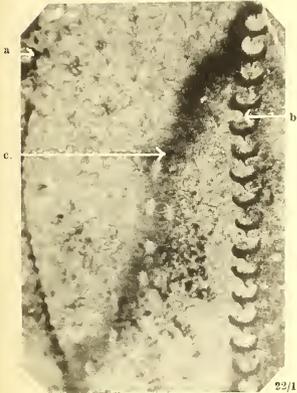


FIG. 23.

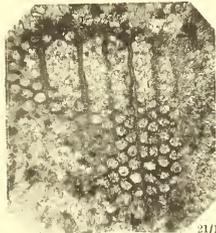


FIG. 21.

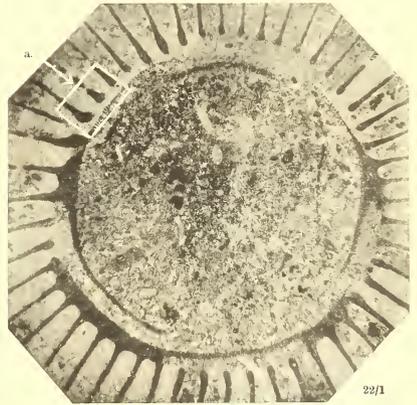


FIG. 19.

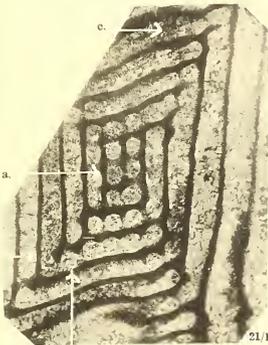


FIG. 22.

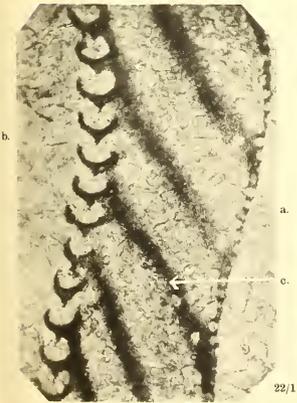


FIG. 24.

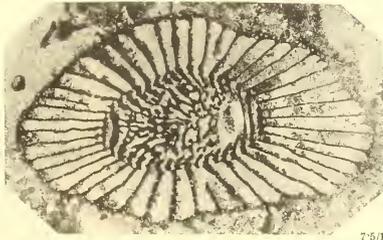


FIG. 25.



FIG. 17.



Dr W. T. GORDON: "Cambrian Organic Remains from Weddell Sea."—PLATE III.



FIG. 27.

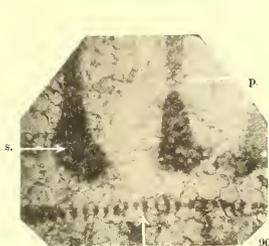


FIG. 26.

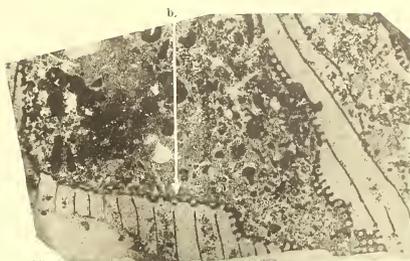


FIG. 28.



FIG. 33.



FIG. 35.



FIG. 30.

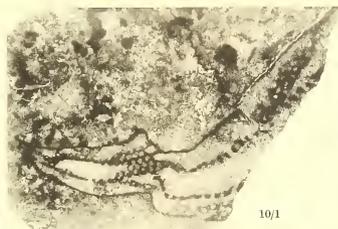


FIG. 31.



FIG. 29.

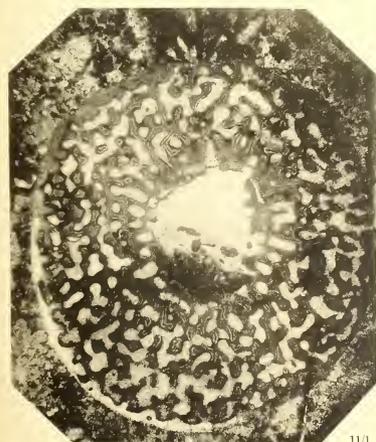


FIG. 32.

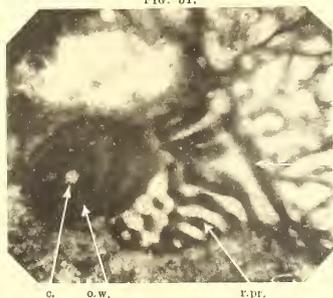


FIG. 34.



FIG. 36.



Dr W. T. GORDON: "Cambrian Organic Remains from Weddell Sea."—PLATE IV.

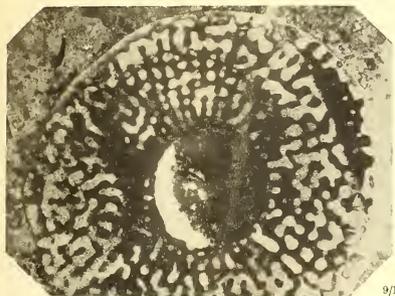


FIG. 37.

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FIG. 39.

9/1

9/1

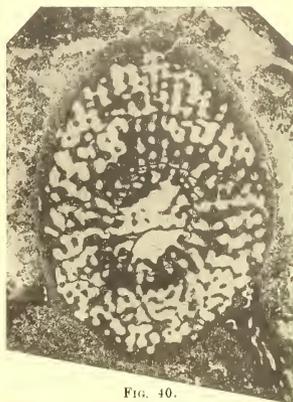


FIG. 40.

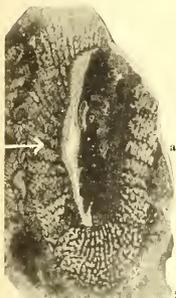


FIG. 38.

2.5/1

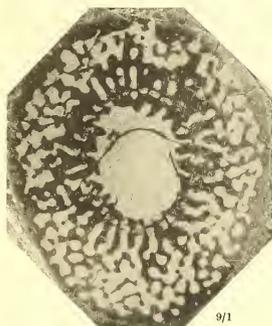


FIG. 41.

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FIG. 42.

9/1

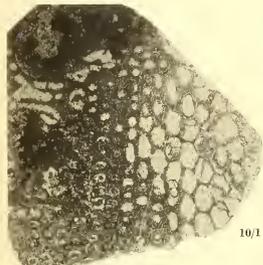


FIG. 45.

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FIG. 46.

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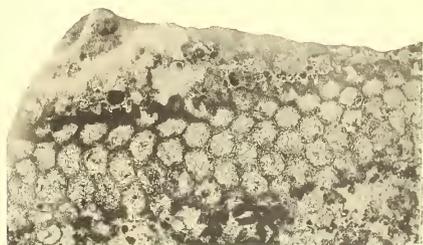


FIG. 47.

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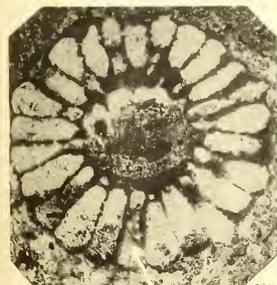


FIG. 43. w. p. p.

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FIG. 48.

10/1

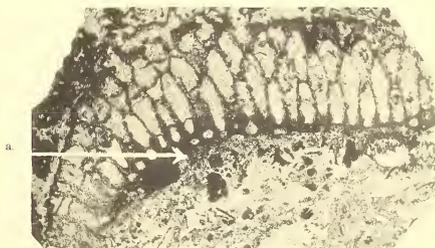


FIG. 44.

10/1





FIG. 49.

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FIG. 51.

26/1



FIG. 55.

9/1



FIG. 56.

25/1

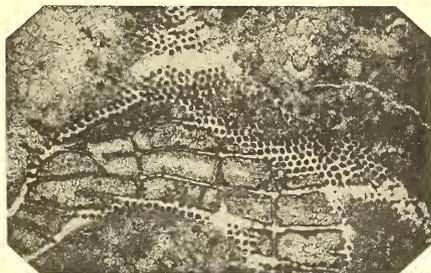


FIG. 54.

9/1



FIG. 50.

5/1



FIG. 52.

9/1



FIG. 57.

9/1

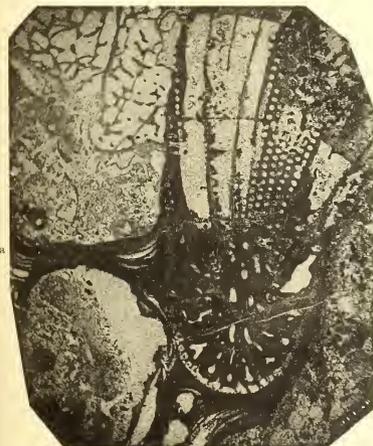


FIG. 53.

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FIG. 58.

5.5/1

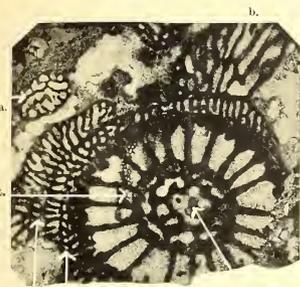


FIG. 59.

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Dr W. T. GORDON: "Cambrian Organic Remains from Weddell Sea."—PLATE VI.



9/1 p. p. FIG. 60. c.t.



FIG. 61. c. 9/1

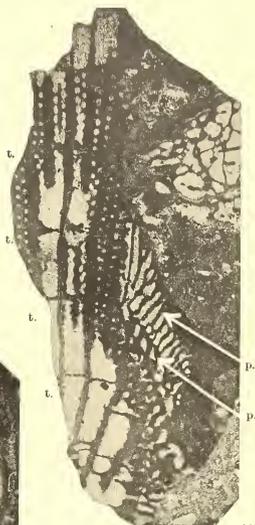


FIG. 62. 9/1

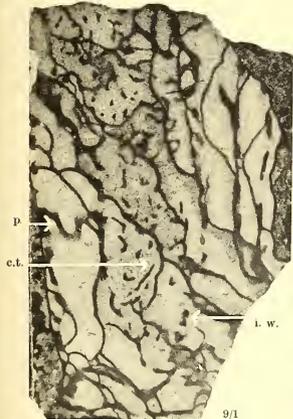


FIG. 64. 9/1



FIG. 63. 9/1



FIG. 67. 11/1

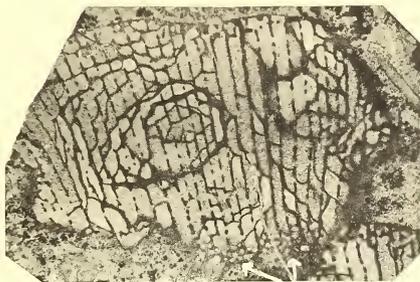


FIG. 69. w. p. 9/1

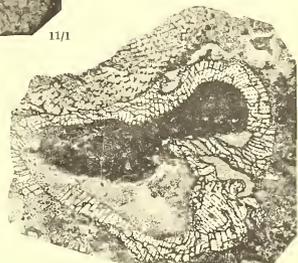


FIG. 68. 3/1



FIG. 71. 9/1



FIG. 70. 27/1

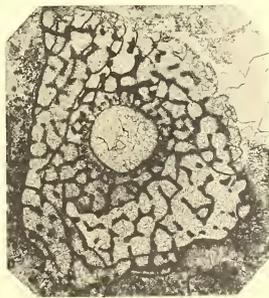


FIG. 65. 9/1



FIG. 66. 3.5/1



Dr W. T. GORDON: "Cambrian Organic Remains from Weddell Sea."—PLATE VII.

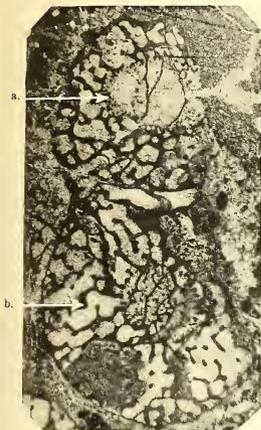


FIG. 72.

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FIG. 76.

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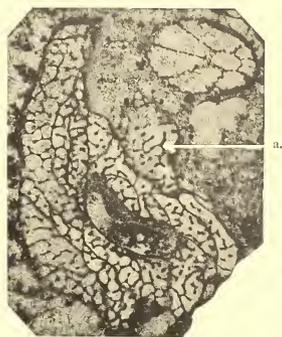


FIG. 75.

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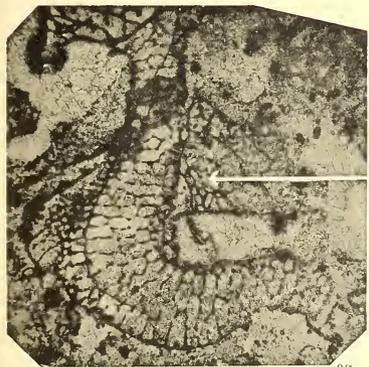


FIG. 78.

9/1



FIG. 77.

9/1

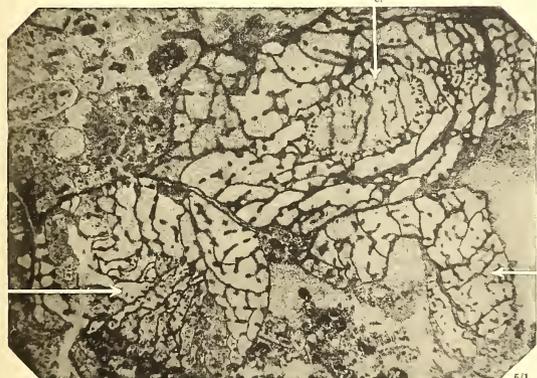


FIG. 73.

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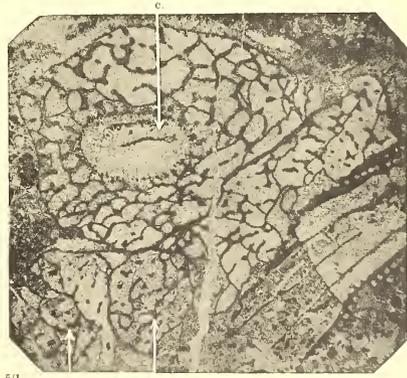


FIG. 74.

5/1



XXVIII.—**New Stelar Facts, and their Bearing on Stelar Theories for the Ferns.** By  
**John M'Lean Thompson, M.A., D.Sc., F.L.S.,** Lecturer on Plant Morphology,  
 Glasgow University. (With Four Plates and Nine Figures in the Text.)

(MS. received March 1, 1920. Read March 1, 1920. Issued separately July 9, 1920.)

For over thirty years problems of stelar structure in the Ferns have claimed the attention of anatomists. By common consent protostely has been recognised as a primitive state. It is seen in all phyla of primitive vascular plants, except the semi-aquatic Equisetales, it figures universally in the juvenile plants of the Filicales, and is maintained in the adult stems of a number of their primitive genera.

But as to the origin of pith, inner phloëm, and inner endodermis, and the steps by which during descent the primitive protostely has in many instances been replaced in the adult by other more complex stelar states, there is no general agreement. On the one hand, the pith, inner phloëm, and inner endodermis have been regarded as purely intrastelar tissues directly referable in origin both in individual plants and descent to the procambial mass of the growing point of the stem. On this view medullation and solenostely are considered consecutive resultants of direct intrastelar readjustments, the steps taken being: (i) an ontogenetic progression from the solid xylem-core of the protostele in the juvenile axis to a medullated protostele by change of destination of procambial elements. These have reached maturity as parenchymatous cells rather than as tracheides; (ii) a further ontogenetic change from the medullated protostele thus established to a solenostele by differentiation of procambial cells as sieve-tubes and endodermis within the pith itself; (iii) the establishment of direct histological connection between the intrastelar pith and the cortex through gaps in the stelar cylinder. On the other hand, the pith has been interpreted as cortical tissue involved in the stele during descent. The pith is considered of purely cortical origin, and the inner phloëm and inner endodermis of the solenostele are held to be extensions of the outer phloëm and endodermis of the original protostele. On this view the steps of progression from protostely to solenostely are: (i) the solid protostele is followed in the ontogeny by a conductive tract into which, from the axil of each leaf-trace, a decurrent mass of cortical tissue intrudes. These cortical masses are lodged in endodermal pockets; (ii) as the ontogeny advances succeeding pockets of cortical tissue are confluent within the stele, their common product being the pith which communicates with the outer cortex through the mouths of the pockets or stelar gaps. By extension of phloëm and pericycle of the protostele during medullation solenostely is attained.

Both views have been held by mutual exclusion for the Filicales as a whole; on the other hand, pith is considered in some cases of intrastelar origin, in others as

cortical tissue. But whatever view is entertained of the origin of pith and other stelar tissues during descent, the ontogeny holds a permanent structural record of the stelar changes which have occurred in each individual organism. These changes are fully revealed only by exhaustive ontogenetic study, but even when they are known it is doubtful how far they recapitulate the stelar changes of the ancestry. On this point light may be shed by the study of related organisms. At the present moment the sum of available ontogenetic evidence is small, and includes fragmentary records. But though supplemented by a large body of fact from adult structure, it is still an inadequate basis for the superstructure of theory which it must bear. The evidences in favour of the view of intrastelar origin of pith are only in a few cases sufficient, while confluence of pockets, on which the theory of cortical origin of pith is founded, has not been demonstrated.

In the following pages new ontogenetic facts are given for a number of Ferns. In some instances these are complete, in others incomplete; but with the structural facts already known they may form a broader basis than has hitherto been available on which to found a stelar theory for the Ferns. It is held that they in no way support a theory of cortical origin of pith, but in each case medullation, and in some cases solenostely arise in the ontogeny entirely by intrastelar readjustment in which a change of proembial destination, as indicated above, is mainly operative. The facts recorded are dealt with in a rough ascending scale, but are not to be interpreted as constituting a strict phylogeny.

*Schizaceæ.*

Stelar Anatomy of the Sporeling of *Schizaa malaccana*, Bk.\*

Figs. 1-6 represent successive transverse sections of the stele of the stem, and are drawn to a uniform magnification. Fig. 1 is from the incomplete base of the stem. In the sclerotic cortex is a leaf-trace (L) which has departed from the lower portion of the stele. It is improbable that this is the first leaf-trace formed for this plant, but for convenience of description it may be referred to as such. The stelar xylem is parenchymatous, and is surrounded by unbroken bands of phloëm (Ph.), pericycle (Pr.), and endodermis (En.). At A the tracheides and wood-parenchyma are segregated, the latter forming a definite mass to the inside of an arc of phloëm and xylem (X), which at a higher level supplies the second leaf-trace. In fig. 2 the second leaf-trace (L) is almost free from the stele. It has departed in the protostelic manner, causing no marked disruption of the stelar xylem, but the stelar phloëm is interrupted. An irregular bridge of endodermal cells (B) partially spans the isthmus between the leaf-trace and the stele. This bridge is completed in sections immediately following the one now figured, and the liberation of the leaf-trace leaves no gap in the endodermis of either leaf-trace or stele. Local segregations of wood-parenchyma

\* The sections on which the following statements are founded are Nos. 1603-1605 in Prof. GWINNE-VAUGHAN'S collection of preparations in the Botanical Department, Glasgow University.

are present, and one of these (A) helps to define the base of the third leaf-trace (X). The departure of the third leaf-trace is shown in fig. 3. The steps taken in the liberation of the second leaf-trace are here repeated; but opposite the leaf-trace not only is the stelar phloëm interrupted, but the xylem is greatly reduced. The chief change of stelar structure at this level is due, however, to a well-defined core of parenchyma within the xylem (M). The sections preceding the one now figured show this pith to be a mass of xylem-parenchyma more extensive and continuous than the masses of similar nature already noted at lower levels. It is a purely intraxyletic tissue in origin as in location. Within it is a group of tracheides (T) which are linked at higher and lower levels to the general xylem mass. The departure of the third leaf-trace is thus protostelic, and pith has been formed within the wood itself. At O a parenchymatous connection links the pith and pericycle. In fig. 4 the departure of the fourth leaf-trace is shown. The stelar endodermis remains an uninterrupted histological barrier between the stele and cortex. Both stelar phloëm and xylem are discontinuous opposite the leaf-trace, and pericycle and pith are in open parenchymatous connection through the intrastelar gap thus formed (O). The closure of this gap is secured in the immediately succeeding sections, and in the internode which follows the parenchymatous pith is increased and is still traversed by groups of tracheides (T, fig. 5). In fig. 6 is shown the stelar structure immediately above the point of liberation of the fifth leaf-trace. During departure of this trace the stelar endodermis is maintained unbroken. At the level figured the pith is composed entirely of thin-walled parenchyma (M), though in the immediately preceding sections it contains scattered tracheides. A parenchymatous gap in the cylinder of xylem and phloëm places the pith and pericycle in direct histological connection, but at a higher level this gap is closed.

The transition thus traced from solid protostely without intrastelar gaps to protostely with a purely parenchymatous pith and intrastelar gaps is shown in the three series of sections of sporeling plants in GWYNNE-VAUGHAN'S collection. In them the isolation of stele from cortex is maintained complete, for until stele and cortex are merged in the procambial mass the stelar endodermis is clearly seen as an unbroken ring around the pericycle. But whatever interpretation may be put upon these stelar changes in the light of adult structure and lateral comparison, in the individual sporelings referred to the following facts are clear:—

- (i) The stelar endodermis is an unbroken cylinder throughout, and no lateral connection between cortex and pith has been observed.
- (ii) The pith is of intrastelar origin, arising in the ontogeny by gradual increase of wood-parenchyma at the core of the stele, with an accompanying decrease of central tracheides. This intraxyletic readjustment can be explained most reasonably as due to change of destination of procambial elements as the growing point advanced.

- (iii) No marked increase has occurred in diameter of the xylem-cylinder or stelar area during the transition from solid protostely to the medullated state. Thus the progression to the well-marked parenchymatous pith is accompanied by reduction in transverse area of wood. The increase of stelar parenchyma is in this instance greater than that of conductive tracheides, the gain to the former constituting a loss to the latter. The interdependence of medullation and xylem-increase, and the intrastelar origin of pith in *Schizæa malaccana*, are thus indicated.

The progression from the juvenile to the adult stele has not been traced, but the latter has been examined by RUSSOW (51), PRANTL (50), TANSLEY and CHICK (58).

They have recorded a stelar structure similar to that shown in fig. 6, and were united in considering the intraxyletic parenchyma "an intrastelar pith." The differentiation of the vascular system from the growing apex of the stem has been studied (58). The recorded facts are in harmony with the intrastelar theory for the pith, and in no way support the cortical hypothesis. Within the pith TANSLEY and CHICK have found in plants with large steles, strands of tracheides the arrangement of which is "quite capricious." Thus the pith with internal tracheides described for the sporeling has been shown to recur in the adult.

To other features which have been observed in adult stems of this species, and particularly the presence of endodermal pockets decurrent from the axils of leaf-traces through xyletic gaps into the pith, further reference will be made. For the moment it may suffice to note that, though the ontogenetic development of these pockets has not been observed, they are absent from the medullated sporeling. It may then be held that in the ontogeny of *Schizæa malaccana* stelar pocketing is antedated by medullation.

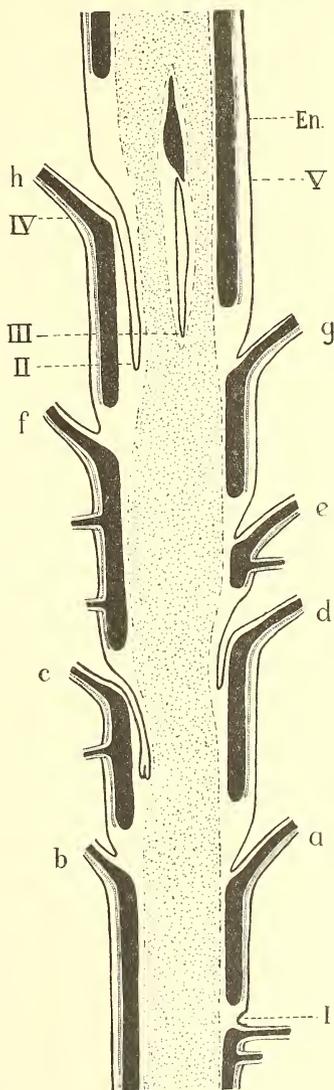
#### *Schizæa dichotoma.*

A number of incomplete adult stems of this species have been examined.\* In general they revealed a stelar structure similar to that already described by BOODLE (3), (5). Throughout the greater length of stem examined the bulky sclerotic pith has a selvage of thin-walled parenchyma. For the most part the xylem-cylinder is solenoxyletic, locally it is dietyoxyletic, and xyletic gaps independent of leaf-traces occur. In text-fig. 1 the general distribution of stelar tissues is shown in longitudinal section with leaf- and root-traces reduced to one plane. Endodermis is indicated by the line (En.), thin-walled-parenchyma is white, phloëm cross-hatched, xylem solid black, and sclerenchyma dotted. Leaf-traces are lettered in ascending order (a, b, c, etc.), and levels specially mentioned are numbered. At I there is a xyletic gap with shallow endodermal pocket, but no leaf-trace. In the axils of leaf-traces a, b, e, f, and g are

\* These have been kindly provided by Professor MARGARET BENSON, D.Sc., and Rev. W. W. WATTS, F.L.S.

shallow endodermal pockets. From the axils of leaf-traces *c*, *d*, and *h*, pockets of varying length are decurrent through xylem gaps into the parenchyma between the xylem-cylinder and central sclerenchyma. These pockets are of varying depth; they are basally closed and contain tissue similar in structure to the inner cortex. In one instance (*e*) the base of the pocket is forked. At III a spindle of endodermis enclosing parenchyma is immersed in the pith. As this spindle dies out it is followed upwards by a growing mass of tracheides, which in like manner dwindles to a vanishing point, leaving the stelar core completely sclerotic. The general distribution of stelar tissues thus noted is similar to that already recorded by BOODLE (5) for this species. Certain points of detail, however, merit special attention. Fig. 7 represents a transverse section of the stele at I, and shows the shallow endodermal pocket already referred to (Pk.). The stelar core is a continuous mass of sclerenchyma separated for the greater part of its circumference from the xylem-cylinder by a selvage of thin-walled parenchyma. At several points this selvage is narrow, and at *S* the sclerenchyma abuts upon the tracheides. At *T* and *U* tracheides are isolated within the selvage, and may thus be in contact with the sclerenchyma. The impression gained from many such sections is that the general distribution of these stelar tissues is fairly defined, but that intrastelar adjustments may occur.

Fig. 8 represents a transverse section of the stele at II. From it, it will be again apparent that, by local increase or decrease of xylem, parenchyma, and sclerenchyma, an histological balance is struck within the stele. That the consequent variations from point to point in the proportions and distribution of the component tissues are purely intrastelar matters cannot be doubted. At *W* a group of endodermal cells is lodged in a mass of parenchyma.



TEXT-FIG. 1.

This is the closed base of the endodermal pocket decurrent from the axil of leaf-trace h, while the base of the trace itself is indicated by the protruding arc of xylem and phloëm (Y). Fig. 9 represents a transverse section of the stele at a slightly higher level (III). Here the endodermal pocket is tubular, and contains thin-walled parenchyma like that of the inner cortex. The stelar core is no longer purely sclerotic, but comprises thin-walled cells (Z), among which endodermal cells occur (En.). These are the basal cells of the endodermal spindle. In fig. 10 the stelar structure at level IV is shown. The mouth of the pocket has been reached, but the leaf-trace is not yet free from the stele. An increased proportion of the intraxyletic tissue is thin-walled parenchyma, here continuous from the stelar core to the pericycle through the xyletic gap (G). At this level the isolated endodermal spindle is a wide tube (En.) containing thin-walled cells like those around it. At V the leaf-trace has been freed from the stele, and the endodermal spindle in the pith has reached a vanishing point (En., fig. 11). Within the central parenchyma is a group of tracheides (T). The succeeding sections show no trace of the inner endodermis, but the inner tracheides are increased in number (T, fig. 12).

Reduction of the xylem spindle marks the succeeding sections. Its vanishing point is reached in fig. 13 (T), and the pith is once more mainly sclerotic.

All the structural facts accord with the view that the intrastelar changes in balance and distribution of wood, thin-walled parenchyma, sclerenchyma, and endodermis, thus traced from point to point, have been accomplished in the ontogeny by change of procambial destination as the growing point advanced, and that the tissues involved are of purely intrastelar nature.

Isolated endodermal spindles within the pith have also been recorded by BOODLE (5), who, for lack of a ready explanation of their function as independent structures, suggested that they may be relics of foliar pockets, which, having figured in the ancestry, have lost their mouths during descent, and thus are no longer linked to the outer endodermis at stelar gaps. TANSLEY and CHICK (58) have recorded not only deep foliar pockets but also an endodermal spindle within the stele of *Schizaea malaccana*. The latter structure is decurrent from the axil of a leaf-trace, but, though devoid of an opening into the cortex, is linked to the outer endodermis through the xyletic gap by a chain of endodermal cells. It is undoubtedly a potential pocket, but its actual state and origin may be variously interpreted. It may indicate a phyletic degeneration of foliar pockets, or may merely illustrate how procambial destination determines mature structure. On the latter view an endodermal spindle initiated within the stele may in one instance be linked to the outer endodermis at a xyletic gap, thus contributing to one unbroken endodermis; in another such an endodermal union may be partial or absent. The central position of the endodermal spindle referred to in the adult stele of *Schizaea dichotoma* and its independence of adjacent leaf-traces give point to the latter suggestion. It is indeed

obvious that a deep pocket is associated with the nearest leaf-trace (text-fig. 1). On this view endodermal cells within the stele may be regarded as new creations, which in some cases form foliar pockets, in others remain isolated structures. But in all instances they provide an increased endodermal area for the stele, and may enhance the physiological control.

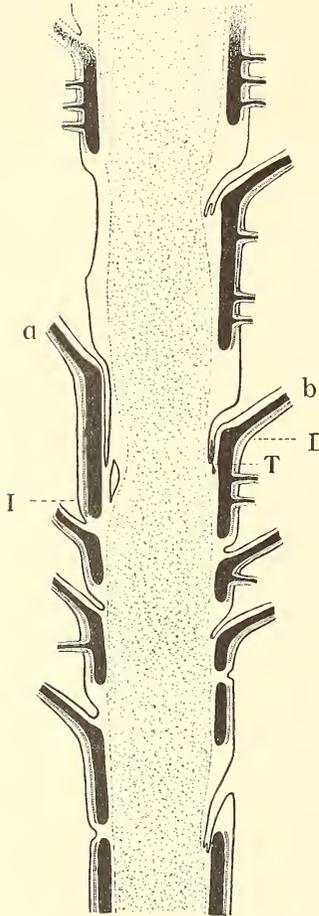
The ancestry of the *Schizæaceæ* is unknown, and accordingly phyletic degeneration of foliar pockets for the stock is matter of mere speculation.

That medullation and pocketing are distinct phenomena in *Schizæa dichotoma* as in *Schizæa malaccana* is evidenced by the sporeling structure described by BOODLE (3). He has traced the transition from solid protostely to medullation by aeropetal increase of wood-parenchyma. The departure of the first leaf-traces is protostelic and, though pocketing is initiated, medullation is independent of it. An isolated endodermal spindle has also been observed in the sporeling pith. When to these facts is added the structural evidence already recorded from sporelings of *Schizæa pusilla* (13), *Schizæa rupestris* (11), and *Anemia phyllitidis* (3), (11), and from adult plants of *Schizæa digitata*, and *Schizæa fistulosa* (3), belief in the intrastelar origin of pith in these organisms is strengthened.

But on the theory of the cortical origin of pith the medulla of these plants "must be regarded as a derivative of the cortex which has become more or less completely sequestered within the stele" (37). This view, as expounded by JEFFREY (30), (33), finds support in histological similarity between cortex and pith. On purely histological grounds exception may be taken to it, for the pith and cortex in both *Schizæa digitata* and *Schizæa dichotoma* are dissimilar. The sclerotic pith-cells of these species have dense mucilagenous contents, and their highly lamellated walls have numerous fine pits (fig. 15). Their chief duty is apparently water-storage. The cortical cells are mainly sclerosed: where the walls are thick, the pits are wide; where the walls are thin, pitting is obscure. The contents of these cells are not apparently mucilagenous, and starch-storage is an evident function (fig. 14). A reasonable view of such facts may be that structural similarity between cortex and pith indicates for them like functions, while histological differences indicate functional differences. Thus, on histological grounds alone a cortical origin for pith cannot be deduced.

The main prop of the theory of cortical origin of pith is, however, cortical intrusion. No ontogenetic evidence of actual intrusion has been advanced for the *Schizæaceæ*, and a phyletic flow of cortex into the stele can only be inferred. But that pocketing is a result of change of procambial destination rather than a phase of cortical intrusion appears to be the natural interpretation of the structural facts. This view may be further supported from the adult stele of *Schizæa dichotoma*. Text-fig. 2 shows the general distribution of stelar tissues in longitudinal section in part of one of the stems examined. Certain xylem gaps have been omitted. Leaf-traces and endodermal pockets are reduced to one plane. As in text-fig. 1, pockets of diverse depth and form are shown, in some cases decurrent from the axils of

leaf-traces, in others through xylem gaps with which leaf-traces are not associated. But the features to which special attention would be drawn occur between levels I and II.



TEXT-FIG. 2.

Between these lies an isolated endodermal spindle, while within the base of a pocket is a chain of tracheides—here represented as a black line (T). On the theory of cortical origin of pith, tracheides would not be expected to figure among the contents of a closed endodermal pocket. In fig. 16 the stelar structure at the base of the endodermal spindle is shown. The xylem is dictyoxyletic, and to the inside of the narrower xylem gap is an endodermal cell (En.), which is the base of the spindle. Fig. 17 represents the structure at a slightly higher level. The xylem gaps have closed, and the endodermal spindle is here tubular (En.). In fig. 18 the apex of the spindle is reached (En.). At En.' is an almost basal section of the pocket from the axil of leaf-trace a, at En'' is a section towards the base of the pocket associated with leaf-trace b. It contains a mature tracheid. The details of this pocket are shown on a larger scale in fig. 19. The endodermis is a complete ring, and contains a parenchymatous cell (P) and a tracheid (T). Fig. 20 shows the structure of the pocket at a slightly lower level. The endodermis here surrounds two parenchymatous cells, and a tracheid forms part of the endodermal ring. The actual base of the pocket is shown in fig. 21. It comprises six endodermal cells, and partly involves a tracheid. Tracheides of the xylem-cylinder are close at hand (T'). Followed down into a lower section (fig. 22), the tracheid in fig. 21 (T) consorts with other tracheides which lie in the parenchymatous selvage. An inclusion of tracheides in endodermal cells has been observed in another stem. In this case the endodermis was an isolated spindle situated in the sclerotic pith. Fig. 23 shows a section through the base of this spindle. The endodermal cells surround a single tracheid (T). Fig. 24 is from a section of the spindle at a higher level; the endodermal ring (En.) is entirely filled with tracheids. From these facts it may be concluded that by static change

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of destination of procambial cells from point to point mature elements of different category may be variously grouped within the stele. To explain them, neither phyletic nor dynamic flow of tissues is necessary, nor indeed is there evidence of the latter.

On the evidence already dealt with the following conclusions are reached:—

- (i) The species considered have in the adult state medullated protosteles.
- (ii) In each the medulla is of purely intrastelar origin.
- (iii) All the evidence shows that endodermal pockets through xyletic gaps are intrastelar structures, and arise by change of procambial destination within the stele.
- (iv) Endodermal spindles partially or completely isolated within the stele may be regarded in some cases as potential and not vestigial pockets, in others as independent though sporadic formations of inner endodermis which has not been continued permanently in the ontogeny.
- (v) By pockets and endodermal spindles the endodermal area for the stele as a whole is enlarged, and physiological control may be enhanced.
- (vi) That the contents of endodermal pockets and the adjacent cortex are commonly of the same histological character may be expected, since they are continuous through the mouths of the pockets. Thus united, they behave as one tissue which need not be expected to resemble the pith either in structure or function.

#### *Gleicheniaceæ.*

Of Gleicheniaceous plants *Gleichenia flabellata*, *Gleichenia pectinata*, and *Platyzoma microphyllum* bear directly on the subject in hand.

The internode of *Gleichenia flabellata* shows a cylindrical stele with a solid parenchymatous xylem-core. At the nodes shallow endodermal pockets associated with the leaf-traces are decurrent within the stele. The ontogenetic development of these pockets has not been traced, but by them the area of stelar endodermis is enlarged. On the view of static procambial change within the stele, the pockets would be considered intrastelar in origin and independent of any possible medullation. On the theory of cortical origin of pith, their contents would be viewed as cortical tissue by confluence of which within the stele any future medullation would be attained.

The ontogenetic evidence for *Platyzoma microphyllum* is still wanting, but the adult stele has been examined (4), (49), (61), (62). It is commonly a medullated cylinder with both outer and inner endodermis, and phloëm only on the outer face of the xylem. It is devoid of leap-gaps and perforations. Thus the pith is completely isolated from the cortex, and the inner endodermis is independent of its outer correlative. JEFFREY (30) has affirmed that the medulla of *Platyzoma* is "in reality

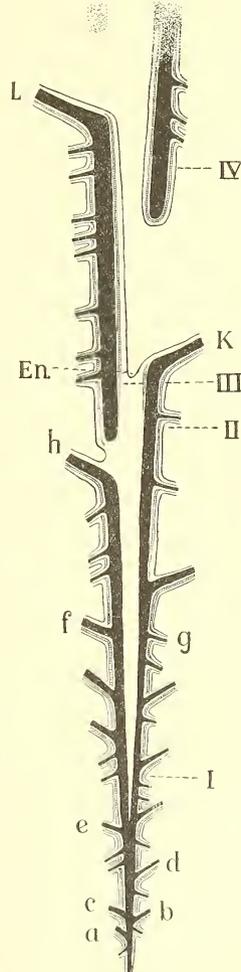
extrastelar, but no longer communicates with the peripheral cortex." For the establishment of this condition he assumed that pocketing had occurred in the ancestry of *Platyzoma*, but that the confluent pockets by which the medulla arose have been "completely cut off from the outside cortex" during descent. It has now been shown that the adult stem of *Platyzoma* is at points protostelic (62); from this state medullation arises by purely intrastelar changes. In like manner, an inner endodermis is developed around the pith. In default of any evidence of loss of stelar gaps and of cortical origin for the pith and inner endodermis, a reasonable interpretation of the adult stelar structure may be that the medulla and inner endodermis are intrastelar in origin as in location. As in *Schizæa malaccana* and *Schizæa dichotoma* so also in *Platyzoma*, the possession of inner endodermis locally or throughout the adult medullated protostele increases the endodermal area, and may enhance the physiological control.

The ontogeny of *Gleichenia pectinata*\* has been studied, and the full facts of progression from the protostele of the sporeling to the solenostele of the adult are now known. At the base of the juvenile plant is a long protostelic tract bearing a number of leaf-traces (a, b, c, d, e, text-fig. 3). A transverse section of the stele at the point of departure of the fourth leaf-trace is shown in fig. 25. There is a solid parenchymatous xylem-core (X), around which the phloëm forms an unbroken ring (Ph.). There is no endodermal pocket in the succeeding sections, and the leaf-trace departs in the protostelic manner. In some of the smaller plants the upper portion of the protostele showed a mixed pith (fig. 26), with large tracheides (T) scattered through thin-walled parenchyma. In some instances the stele was in this condition immediately below the growing point; in others a definite pith existed. In all such cases examined the ontogenetic progression to the mixed pith or pure medulla was marked by segregation of tracheides and parenchyma, as in *Schizæa malaccana*, and the stelar endodermis was maintained unbroken. Thus the pith is an intraxylemic tissue. The protostelic tract of the juvenile axis is followed in the ontogeny by a long medullated stage (text-fig. 3, levels I to II), the central region of tracheides being entirely replaced by parenchyma. At first there are no xylemic gaps at the departure of the leaf-traces or elsewhere. Fig. 27 shows the transverse section of the stele during the protostelic departure of a leaf-trace (f) and a root-trace (g) in this region. Later the xylem is interrupted above the leaf-traces, and opposite the xylemic gaps thus formed there may be slight pocketing of the endodermis (h, text-fig. 3). The ontogenetic stelar changes already traced for *Schizæa malaccana* are thus in general repeated. As the stele is followed forward, phloëm appears in the pith as an indefinite and incomplete ring of sieve-tubes lining the xylem internally (III, text-fig. 3). These are shown at Ph.' (fig. 28), which represents a transverse section of the stele during departure of leaf-trace (k). A solenostelic structure soon follows,

\* The materials for this study were kindly provided by Mr WM. HARRIS, F.L.S., Director, Hope Gardens, Jamaica.

and results from the following steps. Inner endodermal cells appear in the pith (En., fig. 28). These mark the base of a tube of inner endodermis closed below and widening upwards in the pith (En., text-fig. 3). It is continuous on the one hand with the endodermis of the next departing leaf-trace (k), and thus provides the increase of endodermal area which an axillary pocket would secure. It is continued as the inner endodermis lining the internode immediately above (text-fig. 3; and En., fig. 29). In this figure is shown the stelar structure slightly above the point of departure of leaf-trace k. That the tissue which this inner endodermis involves (M, fig. 29) is histologically similar to the inner cortex is matter for no surprise, for they are continuous through a stelar gap and act as one tissue. The stelar structure thus attained is in fact solenostelic. This will be further apparent from fig. 30, which represents a transverse section of the stele at IV (text-fig. 3) after the first leaf-gap is closed. The medulla (M), inner endodermis (En.), inner phloëm (Ph.), xylem-cylinder (X), outer phloëm (Ph.), and outer endodermis (En.) are all shown. Followed upwards, the inner endodermis is continuous with the endodermis surrounding the next succeeding leaf-trace (L, text-fig. 3). In this way the solenostelic structure, once secured, is maintained.

Thus it has been shown that, as in *Schizaea malaccana*, *Schizaea dichotoma*, and others, so also in *Gleichenia pectinata*, medullation and pocketing are distinct phenomena. That medullation antedates pocketing in the ontogeny has indeed been demonstrated. There is no structural evidence of intrusion or flow of cortical tissue by which the pith of the solenostelic tract might arise, and study of the growing point itself supports the view that by change of procambial destination the stelar changes here described are effected. By such a static change alone the continuity of endodermis across the pith could be secured while solenostely is maintained. This formation of inner endodermis follows upon the interruption of the stelar xylem above a leaf-trace (text-fig. 3), which is thus the first associated with a true foliar gap. The immediate result of these changes is the physiological delimitation of the stelar pith of the protostele below the inner endodermis from the later formed pith of the solenostelic



TEXT-FIG. 3.

tract. But that both these tracts of pith are referable in origin to the procambial mass of the growing point seems the only reasonable interpretation of the ontogenetic facts. They are thus viewed as one continuous medullary field across which a barrier of inner endodermis has been constructed by static changes of procambial destination during the ontogeny. Here, as in the other organisms considered, the inner endodermis provides an increase of endodermal area by which the physiological control of the conductive cylinder may be enhanced. Of these organisms *Gleichenia pectinata* is considered the most advanced in stelar structure, the collective attainments of the others in regard to stelar amplification being repeated in its ontogeny. To these are added solenostely and foliar gaps. On the view of static ontogenetic change of stelar structure here adopted, the foliar gaps of *Gleichenia pectinata* are of similar origin to endodermal pockets; but while the latter are closed at their base and do not permit of histological continuity of pith and cortex, the former are open channels through which pith and cortex, originally distinct, unite to form one continuous tissue.

The general position adopted on the facts described is that stelar tissues of any category may be formed where and when required within the confines of the stele. Protostely with medulla, endodermal pockets, and sporadic inner endodermal spindles is the high-water mark attained by intrastelar changes for the species of *Schizæa* dealt with: *Gleichenia flabellata* has acquired endodermal pockets alone, and *Platyzoma* has not advanced to the solenostely shown by *Gleichenia pectinata*, being still devoid of stelar gaps and inner phloëm.

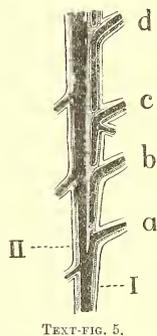
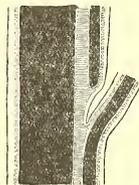
*Gleichenia pectinata* is a solenostelic member of the "Superficiales," thus resembling such organisms as *Metaxya*, *Lophosoria*, *Matonia*, and *Dipteris*, which possess solenosteles and superficial sori. The ontogenetic facts for the latter genera are unknown, but grounds for further comparison may be found in the stelar ontogeny of examples of the "Marginales," which will now be considered.

#### *Lindsaya adiantifolia*.

Facts of adult structure for a number of the *Lindsayas* have been provided by TANSLEY and LULHAM (59), GWYNNE-VAUGHAN, and others. The internode in the *Lindsaya* type shows a dorsiventral stele with parenchymatous xylem-core in which a continuous internal strand of phloëm and parenchyma runs close to its dorsal surface, and is linked to the outer phloëm of both leaf-trace and stele at a xylic gap. These gaps are in the axils of leaf-traces, and through them endodermal pockets are decurrent into the internal phloëm. In the adult stele of a *Lindsaya* the stelar endodermis is thus unbroken. The general arrangement of stelar tissues as seen in longitudinal section is represented in text-fig. 4; xylem is solid black, parenchyma is white, phloëm cross-hatched, and endodermis an unbroken line. The ontogeny of *Lindsaya adiantifolia* opens with a solid protostele. Its xylem-core becomes parenchymatous as it expands (fig. 31). Phloëm forms an narrow unbroken band

in close contact with the wood (Ph.), and the pericycle is broad (Pr.). Text-fig. 5 shows the general arrangement of tissues in median plane of a sporeling. Leaf-traces are lettered, root-traces are on the left, and levels referred to are numbered. Fig. 31 is from level I. At a slightly higher level a mass of parenchymatous cells is seen in the xylem. At the core of this parenchymatous pith sieve-tubes appear in the immediately succeeding sections. This inner phloëm (Ph.', fig. 32) soon bulks largely in the pith, so that the parenchyma around it is reduced to a narrow selvage (S). This is the stelar state at II, a leaf-trace (a, text-fig. 5; L, fig. 32) is departing in the protostelic manner, and towards the upper side of the stele the xylem is thin and commonly interrupted. The number of leaf-traces which depart in the protostelic manner varies from plant to plant, but frequently a xylic gap follows the formation of the first or second trace after inner phloëm is established. Through these xylic gaps inner and outer phloëm may or may not be united. In text-fig. 5 their union is shown through the first xylic gap. There is no structural evidence of intrusion of outer phloëm and parenchyma into the xylem-cylinder, and in these early stages there are no endodermal pockets. The medulla of thin-walled parenchyma and the sieve-tubes are then of intraxylic origin. As the stele is followed forward the arrangement of tissues just described is maintained. This is indicated in the upper portion of text-fig. 5, and inner and outer phloëm are linked through the xylic gaps above leaf-traces b, c, and d. The stelar structure during departure of trace c is shown in fig. 33. The outer phloëm (Ph.) is a narrow band, the inner phloëm is bulky (Ph.'). They are united through the xylic gap before the arc of leaf-trace xylem and phloëm (X) is free. As the stele expands by conical enlargement, the xylic gaps are successively longer. Through them pockets of increasing depth are formed within the stele. Thus the adult *Lindsaya* state is reached.

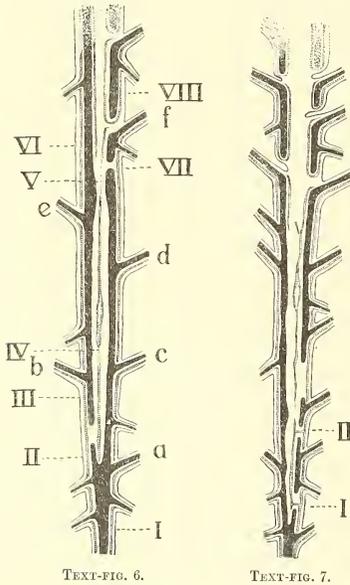
It is thus apparent that in the ontogenetic progression from solid protostely to the adult *Lindsaya* structure, the formation of medulla and inner phloëm involves neither cortical intrusion nor tissue-flow, but is the result of static intrastelar change by which also the pockets in the adult stele arise. The position taken on the structural facts is that in *Lindsaya adiantifolia* medulla and inner phloëm are initiated in close succession at an early stage in the ontogeny. The phloëm is from the first a bulky solid core around which the parenchymatous pith is a narrow selvage. The maintenance of this balance and distribution of stelar tissues with the addition of xylic gaps, endodermal pockets, and phloëm-continuity through the gaps, gives the so-called *Lindsaya* type of adult stele. It is matter for no surprise that the *Lindsaya* state has been recorded for diverse genera, and figures in the early



ontogeny of a number of higher ferns, in which medulla and inner phloëm are early secured; for the *Lindsaya* structure is a stage in intrastelar amplification from an original protostele which may persist into the adult axis, or be passed through to a higher stelar state. The Schizæoid-Dicksonioid affinity of the *Lindsayas* has been indicated by BOWER (11) and others. It will accordingly be of interest to know the ontogenetic facts for a plant of like general affinity but more advanced adult stelar structure. The facts for *Loxsonia Cunninghamii* will now be given.

*Loxsonia Cunninghamii*.

The adult solenostele of this species has been fully described by GWYNNE-VAUGHAN (24). The ontogeny opens with a basal region of protostely of varying



TEXT-FIG. 6.

TEXT-FIG. 7.

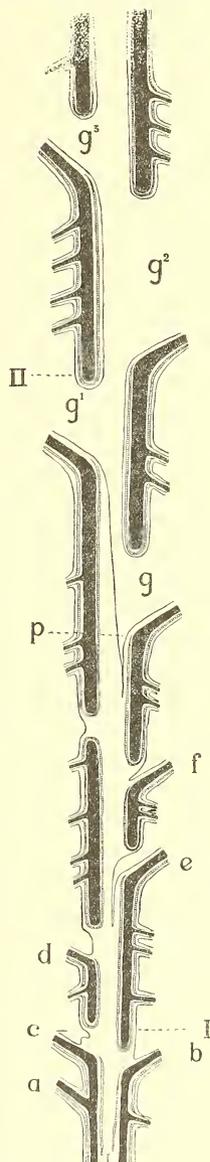
length, and bearing both leaf- and root-traces. The bases of text-figs. 6 and 7 show the general arrangement of tissues in this region; xylem is solid black, parenchyma is white, phloëm is hatched, and endodermis is an unbroken line; leaf-traces are lettered, and levels referred to are numbered. Fig. 34 shows the stelar structure at I, text-fig. 6, and shows the solid protostely. As leaf-trace a is departing a medulla appears. At its core is a strand of sieve-tubes. Fig. 35 shows the stelar structure at this level (II); there is a xylic gap, but the inner (Ph.) and outer phloëm (Ph.) are not united through it. Fig. 36 shows the structure at III; the xylic gap is closed, and the slender core of phloëm persists. For a considerable distance leaf-traces are liberated in the protostelic manner (b, c, d, and e). The pith is well developed, and the central strand of phloëm is locally indefinite, IV and V.

At VI it is tubular, and involves parenchymatous cells. Fig. 37 shows the stelar structure during departure of leaf-trace d, and illustrates the *Lindsaya* condition with protostelic departure of a trace. At VII there is a second xylic gap independent of a leaf-trace. At this level the inner phloëm is indefinite, but no indication of a phloic connection through the gap is seen. As leaf-trace f is departing, the inner phloëm becomes definitely tubular. Above f is a xylic gap through which inner and outer phloëm are linked for the first time. Fig. 38 shows the stelar structure at VIII; the inner phloëm (Ph.) is a tube within the parenchymatous pith. The stele is in this

condition as it merges into the undifferentiated mass of the growing apex. From these facts it may be concluded that by early initiation of inner phloëm within a purely intraxyletic pith a *Lindsaya* structure arises. By change of procambial destination the inner phloëm may vary in amount and position, and the final structure so far evolved for the specimen considered is a medullated protostele with inner phloëm and xyletic gaps, but devoid of endodermal pockets.

In text-fig. 7 the general arrangement of stelar tissues in another specimen is shown. In its essential features it repeats the stelar changes from solid protostely to medullated protostely with tubular inner phloëm, and xyletic gaps recorded from the first plant. The full resemblance to a *Lindsaya* type, as illustrated by *Lindsaya adiantifolia*, lies in the fact that the outer and inner phloëm may be connected through xyletic gaps (I and II). Towards the apex of the stele definite endodermal pockets of variable depth are associated with the leaf-traces. Text-fig. 8 shows the stelar state in part of an adult plant. At the base the inner phloëm is tubular, and a leaf-trace is departing in the protostelic manner (a). Associated with leaf-traces c, d, e, and f are endodermal pockets of variable depth. The pith is bulky, and the inner phloëm is a wide tube more or less coaxial with the xylem-cylinder. Fig. 39 shows the stelar structure at I, and illustrates the stelar expansion which has been effected. Passing upwards, endodermal cells appear in the pith (En', fig. 40). These form the base of a pocket (P, fig. 41; p, text-fig. 8), which opens into the first foliar gap (g; and G, fig. 42), and extends onwards into a succession of them ( $g^1$ ,  $g^2$ , and  $g^3$ ). Thus, as in *Gleichenia pectinata*, a continuous inner endodermis is established, and solenostely is attained. Fig. 43 shows the full solenostelic structure at II. The pith (M) is here a continuous column of more or less sclerotic tissue like the cortex without, to which it is directly linked through the succession of foliar gaps.

No structural evidence has been found of sliding growth or cortical intrusion to which the establishment of solenostely could be referred, but the study of the growing point has led to the conclusion that here, as in other organisms already considered, the successive changes of stelar structure

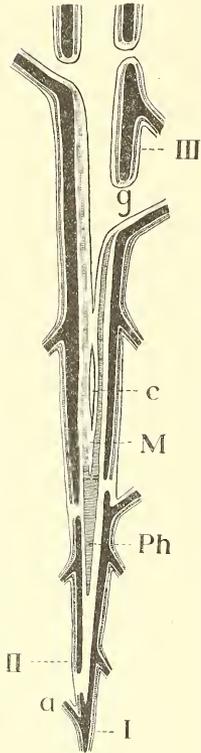


TEXT-FIG. 8.

from protostely to solenostely are due to a static change of quality of procambial cells as the growing point advanced.

*Acrostichum aureum*.\*

In *Loxsoma* the internodes are long, and solenostely is delayed until many leaves have been formed. But in many ferns with upright stocks the internodes are short, and certain ontogenetic steps are apt to be abbreviated or even omitted. This may be illustrated by *Acrostichum aureum*, a plant of Pterid affinity. Text-fig. 9 shows the arrangement of stelar tissues in the juvenile axis of a sturdy plant. The stage of solid protostely is brief (I), only one leaf-trace departing in the protostelic manner before medullation occurs (a). As the stele expands upwards, a medullated stage with a xylic gap is reached (II). Higher up a core of phloëm appears in the pith (Ph). At first it is solid, but later is tubular and encloses parenchymatous pith (M). In the latter an inner endodermis is initiated, as in *Gleichenia pectinata*, *Loxsoma Cunninghamii*, and others considered (e). It is held to be potentially the base of the pocket which opens into the first leaf-gap, but is not maintained and dies out as a spindle when followed upwards. Higher up an inner endodermis is permanently established, beginning as a pocket opening on the one hand into the first leaf-gap (g), and on the other being continued as the inner endodermis of a typical solenostele (III). Thus in the ontogeny of *Acrostichum aureum* the *Lindsaya* stage is brief, and endodermal pocketing is omitted from the early solenoxyletic stages. That its omission goes hand in hand with the early attainment of solenostely is the view here adopted. In some of the specimens examined solenostely arises even earlier in the ontogeny than in the example described. In them isolated spindles of inner endodermis do not occur, but solenostely is secured with the first formation of inner endodermis within the pith. The ontogenetic condensation thus shown for *Acrostichum aureum* appears also in *Cheilanthes*, and in *Pteridium aquilinum* (33),



TEXT-FIG. 9.

(48), and *Pesia podophylla* (11), and may be expected to figure generally for plants of Pterid affinity.

There is already a body of ontogenetic facts which are known for a number of genera. The early stages of the sporeling of *Anemia phyllitides* have been described by BOODLE (3), but the actual transition to solenostely was not traced.

\* The materials on which this study was made were kindly provided by Professor I. B. BALFOUR, F.R.S.

*Osmunda regalis* has been studied in the sporeling stages by LECLERC DU SABLON (48), JEFFREY (33), GWYNNE-VAUGHAN (27), and SINNOTT (55), while FAULL has provided the facts of sporeling structure for *Osmunda cinnamomea* (23). SEWARD and FORD have performed a like service for *Todea* (54).

BREBNER (12), CHARLES (17), and FARMER and HILL (21) have described the sporeling structure of members of the *Marattiaceæ*; while LANG has studied in detail certain of the *Ophioglossaceæ* (43), (44), (45), (46), (47). The facts for *Alsophila* have been described by GWYNNE-VAUGHAN (25), for *Doodia aspera* by CHANDLER (16), and for *Pteridium aquilinum* by LECLERC DU SABLON (48) and JEFFREY (33). All these, with the records of adult structure for a wide range of Ferns (see Bibliography), may easily be freed from the theoretical statements which cling around them. When this is accomplished, they are easily brought into line with the stelar facts recorded in these pages, and are most reasonably interpreted as illustrative of a process of static change of procambial elements by which stelar changes are affected. On this view it is held that the sum of the ontogenetic evidence so far obtained for the Ferns shows that medullation and the solenostelic and dictyostelic states arise in the ontogeny entirely by intrastelar readjustment in which change of procambial destination is mainly operative.

The object of the present memoir is to provide structural facts, but the meaning of stelar change will be dealt with latter. A list of the publications which appear to bear most directly on the subject of stelar development is appended.

#### SUMMARY.

1. The object of this memoir is to provide the ontogenetic facts of stelar development for a number of Ferns.

2. The sporeling structure of *Schizæa malaccana* is first dealt with. From serial sections it is concluded that the pith is of intrastelar origin.

3. A number of incomplete adult stems of *Schizæa dichotoma* have been examined in serial sections, and the stelar structure reconstructed. From these it is concluded that this species has a medullated protostele, the medulla being of purely intrastelar origin. Endodermal pockets in this species are held to be intrastelar structures which arise by change of procambial destination within the stele.

4. The ontogenetic progression from protostely to solenostely is described for *Gleichenia pectinata*, *Loxsoma Cunninghamii*, and *Acrostichum aureum*, and the evolution of the *Lindsaya* type of stele is traced in *Lindsaya adiantifolia*. It is held that in these, medulla and inner phloëm are of purely intrastelar origin, and that the inner endodermis and solenostelic structure of the adult stele of the former species arise by purely static change of quality of procambial elements as the apex of the stem advances. There is no evidence of intrusion of cortical tissues into the stele during medullation.

5. It is held that the sum of the ontogenetic evidence so far available for the Ferns shows that medullation, and the solenostelic and dictyostelic states arise in the ontogeny by intrastelar readjustment in which change of procambial destination is mainly operative.

#### DESCRIPTION OF FIGURES IN TEXT.

In these the general arrangement of stelar tissues is given in median longitudinal section, with leaf- and root-traces reduced to one plane. Leaf-traces and stelar gaps are lettered, and levels referred to are numbered.

Fig. 1. *Schizaea dichotoma*, plan of stelar construction in an adult stem. Outer endodermis, En.; phloem, cross-hatched; xylem, black; sclerenchyma, dotted; parenchyma, white. There are endodermal pockets of varying depth, and isolated spindles of inner endodermis and wood in the sclerenchyma.

Fig. 2. *Schizaea dichotoma*, plan of stelar construction in an adult stem. There is an isolated inner endodermal spindle in the thin-walled portion of the pith, and tracheides (T) are lodged in the bottom of an endodermal pocket.

Fig. 3. *Gleichenia pectinata*, plan of stelar construction in a juvenile plant.

Fig. 4. *Lindsaya aliantifolia*, plan of stelar construction at an adult node.

Fig. 5. *Lindsaya aliantifolia*, plan of stelar construction in a juvenile plant.

Figs. 6, 7. *Loxosoma Cunninghamii*, plan of stelar construction in two juvenile plants.

Fig. 8. *Loxosoma Cunninghamii*, plan of stelar construction in the upper portion of a juvenile plant which has attained a solenostelic structure towards its apex.

Fig. 9. *Acrostichum aureum*, plan of stelar construction in a juvenile plant.

#### DESCRIPTION OF FIGURES IN PLATES.

##### PLATES I-IV.

Figs. 1-6. *Schizaea malaccana*. Transverse sections of the stele of *Schizaea malaccana*, at successive levels in a juvenile plant. 1 is from the protostelic base with solid xylem-core; 6 is from a level transitional to the adult stem, and shows the well-developed pith. A, xylem parenchyma; B, endodermal bridge; En., outer endodermis; L, leaf-trace; M, pith; O, parenchymatous gap in xylem; Ph., phloem; Pr., pericycle; T, tracheides in the pith; X, xylem. (All  $\times 40$ .)

Figs. 7-23. *Schizaea dichotoma*.

Figs. 7-13. Transverse sections of the stele of adult specimen, reconstructed in text-fig. 1. The sections are from successive ascending levels referred to in the text; En., inner endodermis; G, xylic gap; Pk., endodermal pocket; S, sclerenchyma abutting on tracheides; T, U, isolated tracheides; W, base of endodermal pocket; Y, base of leaf-trace; Z, parenchymatous part of pith. (All  $\times 50$ .)

Fig. 14. Transverse section of inner cortex of an adult plant. ( $\times 80$ .)

Fig. 15. Transverse section of sclerenchyma of pith. ( $\times 80$ .)

Figs. 16-18. Transverse sections of the stele of an adult plant, reconstructed in text-fig. 2. The sections are from successive descending levels referred to in the text; En., inner endodermis; En', En'', bases of endodermal pockets. (All  $\times 50$ .)

Figs. 19-22. Transverse sections of pocket En'', text-fig. 2, at successive descending levels until the pocket is closed. P, enclosed parenchyma; T, enclosed tracheides which form a spindle situated partly in the endodermal pocket and partly in the thin-walled selvage and continuous through the endodermis from the one to the other; T', adjacent tracheides in the selvage. (All  $\times 80$ .)

Figs. 23-24. Transverse sections of an isolated spindle of inner endodermis in the sclerotic pith of an adult stem; En., the endodermis; T, enclosed tracheides. (All  $\times 80$ .)

Figs. 25-30. *Gleichenia pectinata*. Successive transverse sections from the protostelic base to a solenostelic tract of a juvenile plant reconstructed in text-fig. 3. En., inner endodermis; En., outer endodermis; M, pith; Ph., inner phloëm; Ph., outer phloëm; T, tracheides in a "mixed-pith"; X, xylem. (All  $\times 45$ .)

Figs. 31-33. *Lindsaya aliantifolia*. Successive transverse sections from the stele of a juvenile plant reconstructed in text-fig. 5. Fig. 31 is from the base; fig. 33 is from a level showing the full "Lindsaya" structure. L, leaf-trace; Ph., inner phloëm; Ph., outer phloëm; Pr., pericycle; S, parenchymatous portion of pith; X, base of leaf-trace. (All  $\times 50$ .)

Figs. 34-43. *Lorsoma Cunninghamii*. Transverse sections of the stele of juvenile plants at successive ascending levels referred to in reconstructions (text-figs. 6, 7, and 8). They show the transition from the protostelic base (fig. 34) to the full solenostelic structure of the adult (fig. 43); En., inner endodermis; G, leaf-gap; M, pith; P, pocket; Ph., outer phloëm; Ph., inner phloëm. (All  $\times 50$ .)

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In the following list of titles no attempt has been made at completeness, but works on stelar anatomy bearing directly on the subject of this memoir alone are cited.

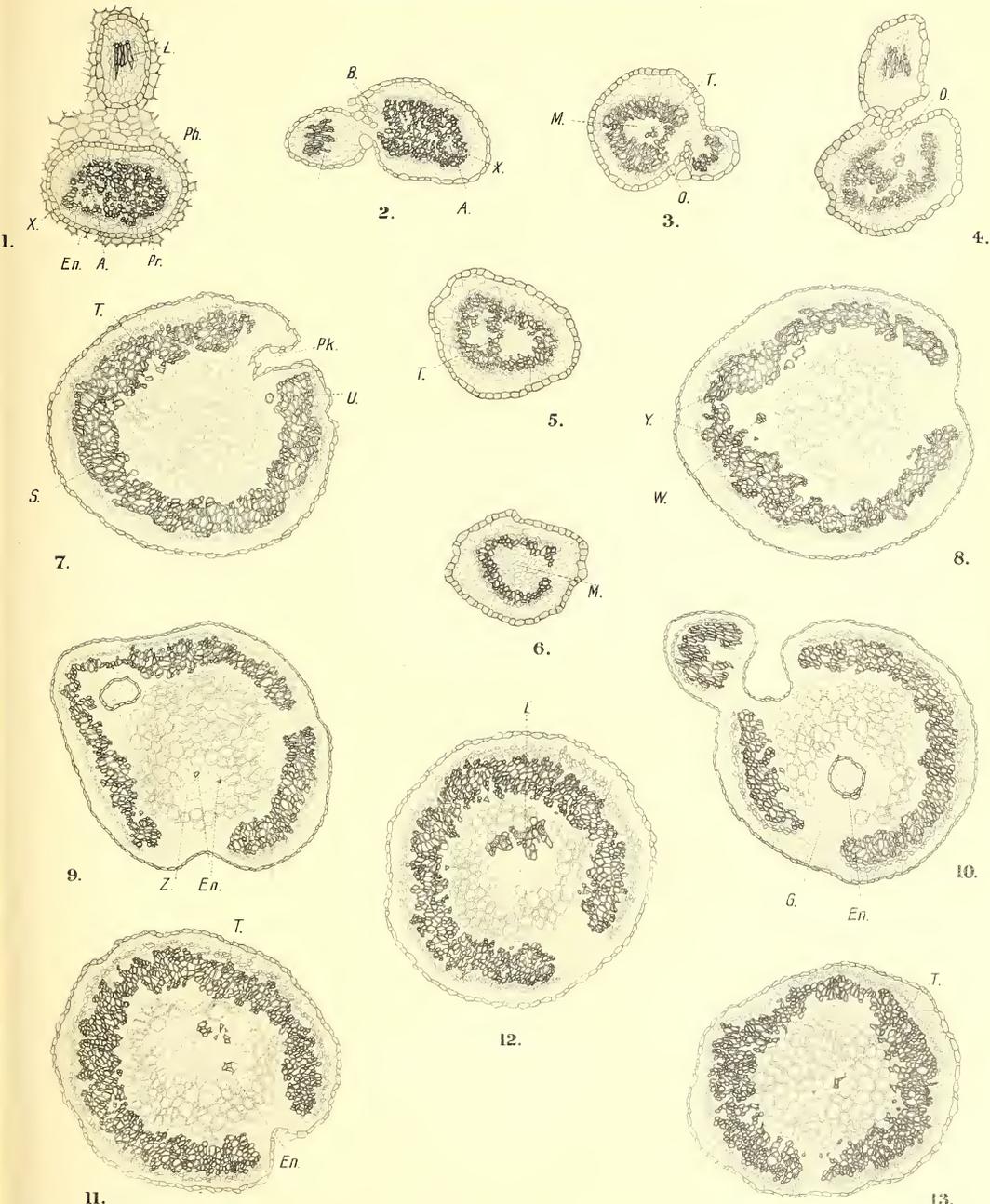
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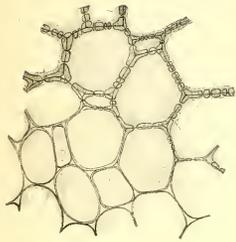


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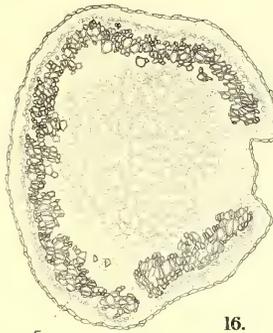




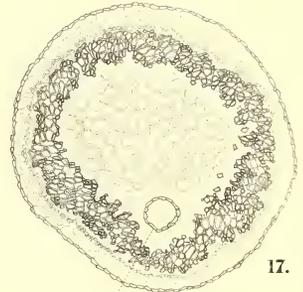
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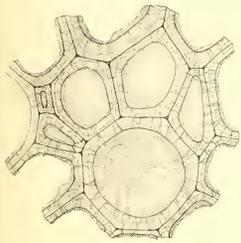
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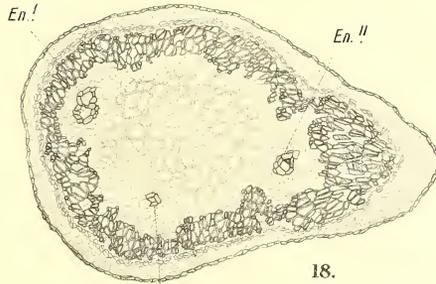
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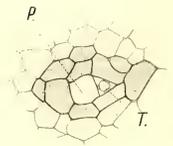


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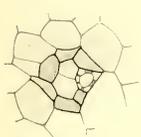
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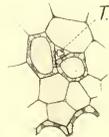


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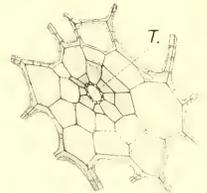
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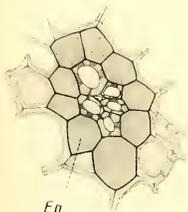
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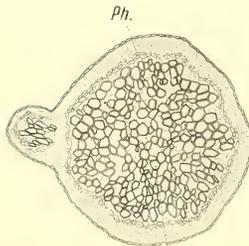
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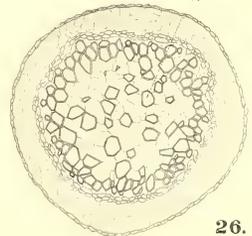
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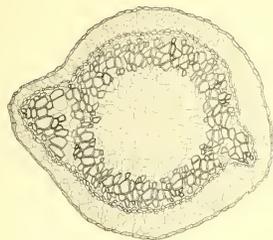


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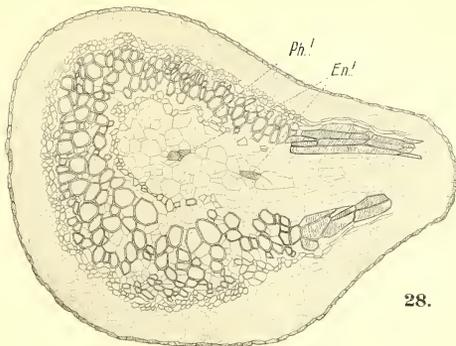
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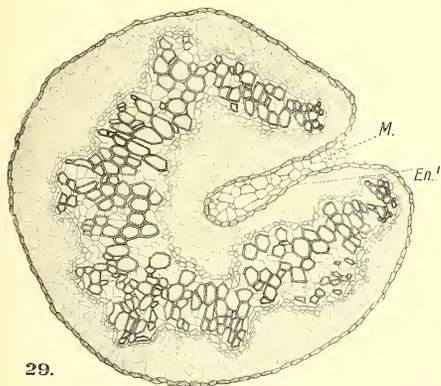
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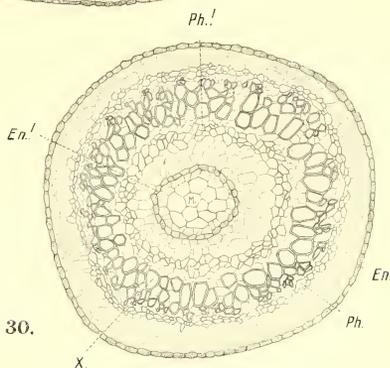
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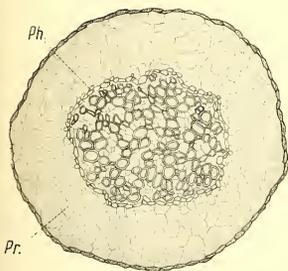
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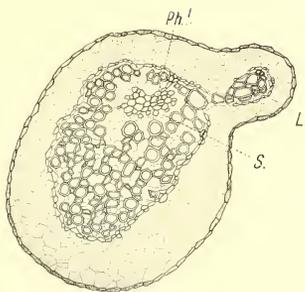
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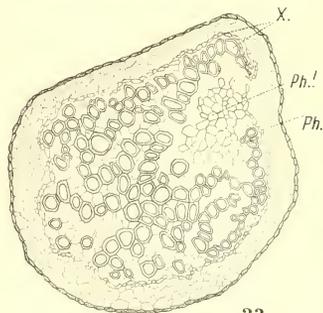
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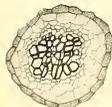
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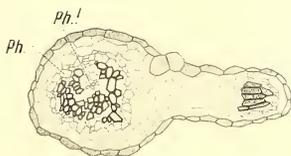
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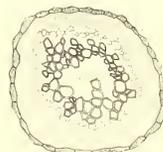
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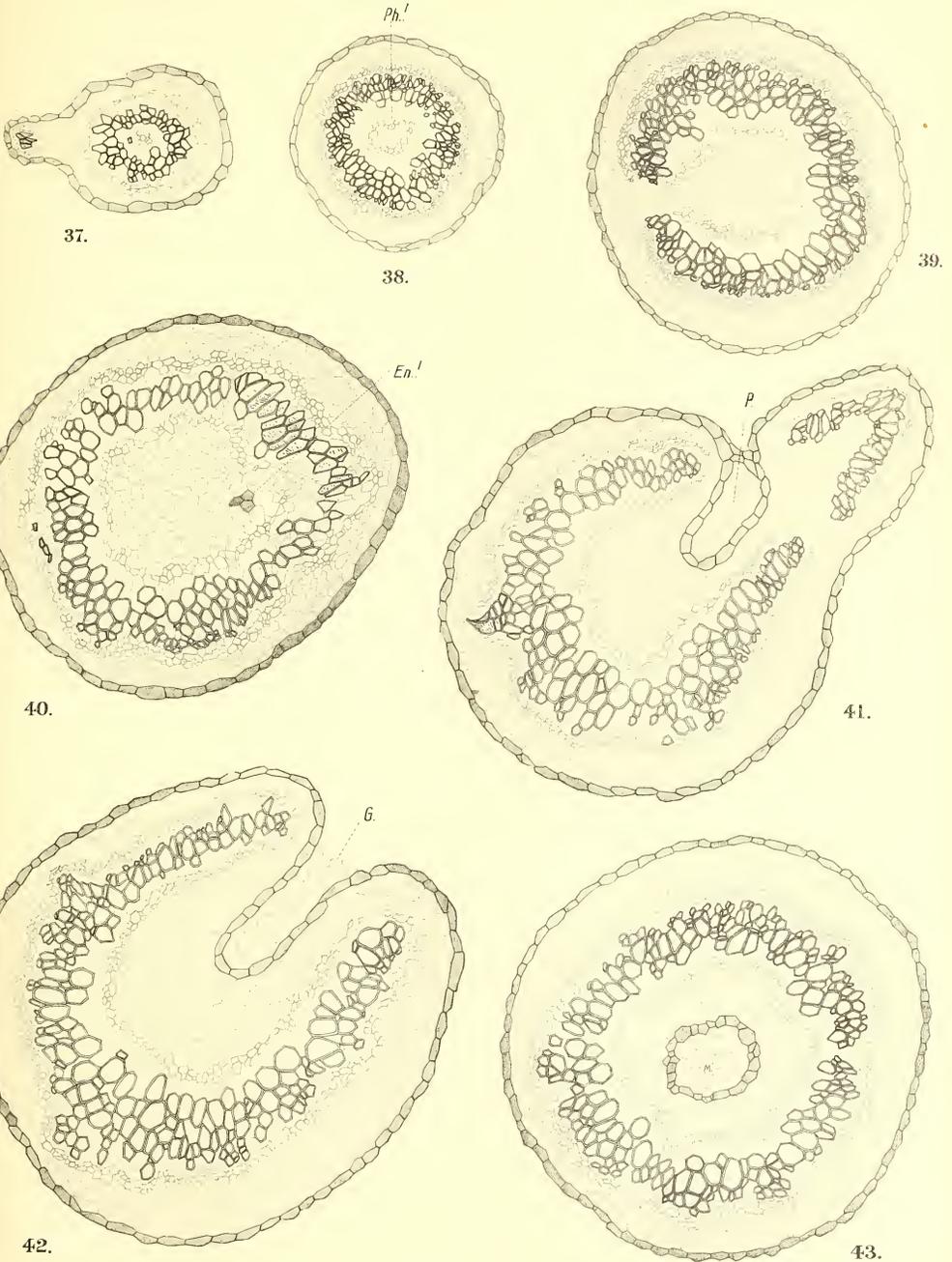
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## XXIX.—ISLE OF WIGHT DISEASE IN HIVE BEES.

- (1) The Etiology of the Disease. By John Rennie, D.Sc. ; Philip Bruce White, B.Sc. ; and Elsie J. Harvey. (With One Plate.)

(Read November 1, 1920. MS. received December 4, 1920. Issued separately March 25, 1921.)

## INTRODUCTORY.

Isle of Wight Bee Disease has been known in this country certainly since 1904, when it was first recognised in the island from which it derives its popular name. According to IMMS it was probably present in Derbyshire in 1902, and was also known in Cornwall and other districts in 1904. Prior to these dates periodic losses of bees of a serious character are on record, dating as far back as the middle of the eighteenth century. BULLAMORE and MALDEN (1912) have summarised fully these outbreaks in historical series in their report in *Journal of Board of Agriculture*, Supplement 8, xix. From a study of the records which they have brought together and from personal inquiries which we have made at various bee-keepers of wide experience, it would appear that none of these earlier outbreaks attained the general distribution throughout the country which we know in Isle of Wight Disease at the present date, nor did any of them remain established over such an extensive period of years as that which has continued without interruption from 1902 until the present time.

Another striking characteristic, and one which has an important bearing in any investigation which seeks to trace the source of this malady, is the fact that no disease of such a permanent and extensive nature has so far been recognised unmistakably outside the British Isles. All the facts we are at present aware of suggest its definitely localised and insular character.

Since 1907 investigations into the cause of this disease have been carried out by a series of workers who have from time to time reported upon the subject: IMMS (1907), MALDEN (1909), GRAHAM SMITH, FANTHAM, and others (1912 and 1913) in England; and ANDERSON (1916), ANDERSON and RENNIE (1916), RENNIE and HARVEY, No. 1 (1919) and No. 2 (1919), in Scotland.

The net result of these investigations has been that the English workers (GRAHAM SMITH *et alii*, 1912 and 1913) put forward as the causal organism the protozoan, *Nosema apis*. It is due to ANDERSON amongst the Scottish workers to state that he was the first to call this conclusion in question, and we think that the later work referred to above (ANDERSON and RENNIE, and RENNIE and HARVEY, 1919) has succeeded in establishing (1) that Isle of Wight disease and *Nosema* infection are not coincident, and (2) that there exists a distinct disease due to *Nosema apis*, which

exhibits, however, totally different external symptoms and a distinct pathology in the individual bee. Collateral work by G. F. WHITE (1918) in America supports this latter conclusion. The problem of the cause of Isle of Wight disease until now has thus been left unsolved.

#### CHARACTERISTICS OF THE DISEASE AS HITHERTO OBSERVED IN THE COLONY AS A WHOLE.

The diagnosis of Isle of Wight disease from "symptoms" has always been a more or less unsatisfactory procedure. Hitherto the presence of the disease in a colony has not been recognised until infection has been well advanced in a high proportion of the bees. At this stage of disability, the most usual features recognisable by the bee-keeper are inability to fly, accompanied sometimes with imperfect folding of the wings. In fine weather a proportion of the affected bees may leave the hive and crawl around, climbing grasses, etc. Later, in the cooler part of the day, they commonly collect in small clusters. Such bees are lost to the colony, since they do not return to the hive, and in any case are useless as workers at this stage. Sometimes large numbers come out and loiter on the alighting board in the sun, returning to the hive when the sun has gone. Associated with the incapacity for flight there is usually a congested condition of the colon. In certain circumstances dysentery may be present as a complication. Most of these symptoms may be present in other disorders of a more temporary kind, and we have been accustomed to regard as true Isle of Wight disease only those cases where such visible conditions, once commenced, continued in the stock, affecting succeeding broods of bees. There is a continuous mortality from the disease. BULLAMORE and MALDEN regard no single symptom as characteristic, and state that "the only essential feature is the death of large numbers of bees."

The association of the causative organism now to be considered will henceforth afford an exact means of diagnosing the disease, which we suggest should now be designated Acarine disease.

#### DISCOVERY OF THE CAUSAL AGENT OF ISLE OF WIGHT DISEASE.

The present and following papers announce the discovery of a parasitic organism invading the respiratory system of the adult bee, which after exhaustive investigation we now bring forward as the causal agent in this disease. This parasite is a hitherto undescribed mite, identified by one of us (J. R.) as belonging to the genus *Tarsonemus*. It was first observed by one of us (E. H.) in December 1919, when a single example was found in a portion of trachea present in a preparation, permanently preserved, of the thoracic glands (fig. 1).\* It was significant of the fuller knowledge of the disease, soon to be attained, that the bee in which it occurred was

\* This find was followed up at the time by a systematic search for mites in hives, upon frames, bees, etc., which resulted in the finding of no fewer than five different species in definite association with bees, dead and alive. (J. R.)

“healthy” in the sense that it belonged to a colony which had no history of disease and was regarded as free from such. In the following May, Mr WHITE made the further and independent discovery that mites in all stages of development occurred in certain of the major thoracic tracheæ of “crawling” bees. In reporting this discovery he stated that he had found this condition in at least 150 sick bees, representative of several diseased stocks, and also that he had failed to find mites in 95 per cent. of apparently healthy bees.\* On this occasion he expressed the view that the parasites seen by him bore a definite etiological relationship to the disease.

That this discovery was one of very great significance was obvious, and the senior author immediately proceeded to its further verification. The first stock of bees examined was one in a highly prosperous condition. The bees were occupying twenty frames in the latter half of May; they were working splendidly and a source of great satisfaction to the owner. Twelve flying bees were captured as they entered the hive. They were taken to the laboratory and the first bee opened was found to contain the parasite in limited numbers. All the twelve were examined, and of the remaining eleven, one other was found also to be harbouring the mite in question.

These facts presented, as in a nutshell, the problem confronting us. It was evident that the distribution was not limited to those bees or stocks hitherto regarded as “sick,” and as the result of the extensive investigations which followed and which are now recorded, we are able to announce that notwithstanding variations in the course of the disease in different stocks, we regard it as established that there is an invariable association of the parasite with diseased stocks, and that there is a definite pathology in relation to infection in the individual bee.

#### INCIDENCE OF INFECTION WITHIN THE COLONY.

*Brood.*—Except in one doubtful case we have not found infection with *Tarsonemus* in brood of any stage, nor has it been found amongst the very youngest of adult bees.

*Workers.*—Amongst workers the infection is most marked in the older bee, and in any case it has not been found except in incipient stages amongst nurse bees whose adult life has been brief.

*Drones.*—We have found that drones of affected stocks suffer equally along with the workers.

*Queens.*—The important and interesting question of the relation of the queen in this connection has been investigated by one of us (J. R.) in a limited number of cases. Of fifteen queens examined of stocks known to be affected with this disease, ten were found to be free, whilst the remaining five harboured this organism. That queens may undergo infection is specially interesting, in view of the familiar fact that the

\* The systematic examination which followed showed the number of apparently healthy stocks harbouring the parasite to be as high as 36 per cent. (J. R.)

queen of an infected Isle of Wight diseased stock survives usually until the colony is extinct. That her survival is in a measure due to the fact that she remains within the hive, is supported by the knowledge we already possess that workers affected with the disease may live for months after they are incapable of flight, and are thus useless to the colony.

#### REGION OF INFECTION WITHIN THE BEE.

The mite, *Tarsonemus*, occupies a very restricted region in that part of the tracheal system which has its origin at the anterior thoracic spiracle. In a well-established case of infection it will be found that, extending inward from this spiracle on either side indifferently, parasites in all stages of development may be present in any part of this portion of the respiratory system, whilst the ill effects of their presence may be seen not only in the region of occupation, but in the muscular tissue to which these extend. It is not an infrequent occurrence in advanced cases of the disease for these wider tracheæ to be occupied with mites in closely packed formation. All stages of development occur; e.g. ova, larvæ, nymphs, and adults may be found together (figs. 2 and 5). In the smaller branches frequently these are occupied as far as their diameter will permit, when a single individual may be found practically blocking the tube, and sometimes a linear succession of individuals may be seen in such a position.

The facts which have led us to the conclusion that the occurrence of this organism in the position indicated is to be regarded as causally related to this disease, are to be found not alone in the presence of *Tarsonemus* in the respiratory system of the bee. There is the universal coincidence of its occurrence in diseased bees. Further, we have been able to trace the development of the disease within bee colonies from the earliest stages of infection to its complete manifestation in crawling and other definite symptoms. We have observed that the total effects resulting from its development, feeding upon the bee and life generally within it, renders it useless as a working unit, disorganises the social system and eventually shortens the bee's life. Further, these vital effects are accompanied by visible pathological conditions in the tissues. The most obvious of these is a browning or blackening and thickening of the tracheal wall (figs. 6 and 7). The thickened tracheæ become progressively hardened and brittle in texture, and certain muscle fibres become atrophied. This latter aspect of the problem is the subject of separate detailed treatment in the paper which follows by Mr WHITE.

These pathological appearances in an infected bee may be present on both sides of the anterior tracheal system. What we have described is the condition in a well-established instance where breeding has been in progress for some time, but as has been mentioned early stages of infection have been frequently witnessed in which the number of parasites present have been observed to be as few as a single mite and no abnormal condition apparent.

CUMULATIVE EVIDENCE THAT *TARSONEMUS* IS CAUSALLY RELATED  
TO THIS DISEASE.

In the course of our investigation we have searched over three thousand individual bees representing 250 separate stocks scattered throughout Great Britain. These examinations covered over 110 stocks reported to us by reliable bee-keepers or certified by ourselves as suffering from Isle of Wight disease. The parasite was present in every one of those stocks. A striking result of this part of the inquiry, which involved the examination individually of 700 bees at least, was the discovery that in every case showing the familiar symptoms of Isle of Wight disease the parasite was present. No exception has been found. There is apparently an invariable and clear association of this organism with all bees suffering from Isle of Wight disease.

These examinations applied not only to bees obtained during 1920, but included samples representative of all seasons of the year, and dating back as far as September 1916. These observations relating to the earlier dated bees were made upon diseased bees which had been preserved by RENNIE and HARVEY on the dates mentioned (see p. 752).

## REPUTED HEALTHY STOCKS.

Amongst the 250 stocks above mentioned there were about 50 which were reported to us as healthy and in which we found the parasite *Tarsonemus* to be present. That is to say, of 140 stocks believed by the owners to be healthy, 50, or nearly 36 per cent., harboured this parasite. Concurrent with such discoveries we ascertained by direct examination ourselves of flying bees (1) which were members of colonies in which the disease was definitely established and (2) which were taken from colonies believed to be healthy and showing no indications otherwise, that amongst these were to be found considerable numbers harbouring the parasite. This was further complicated by the fact that in those infected flying bees certain of those pathological conditions—*e.g.* the blackening and hardening of the tracheal tubes—were very marked. As an example it may be quoted that this condition was found in bees entering the hive carrying pollen or nectar, both belonging to stocks in which crawling and other symptoms were well established, and also to those reputed healthy stocks.

## A PARTICULAR CASE.

As an illustration of this aspect of the disease we may quote the following :—

At the door of the hive of a sick stock showing habitual crawling in fine weather and steadily declining from the disease, we captured as they alighted 27 foraging bees in the course of a single afternoon. *Tarsonemus* was found in every one of these bees, all stages of development being represented. In a number of the cases, soiling and destruction of the tracheal tubes was very marked, quite as bad as anything we have observed in bees crawling from the disease.

In several other stocks showing the disease in an advanced stage, every bee taken over a period extending to weeks, including drones, flying and crawling workers, was found on examination to be infected. The flying workers were frequently more heavily parasitised than were the bees of the same stock which were unable to fly.

These facts have shown us that "crawling" is only one of the phases of the disease and that it cannot be dependent exclusively upon the intensity of the infection, as shown by numbers of parasites; it may be incidental, in part at any rate, to a critical position of certain of the mites, so that oxygen starvation of groups of fibres of the muscles of flight results. Evidence in support of this is brought forward in Mr WHITE's paper which follows, where also other possible factors are considered.

The following Table summarises the typical results of our examinations of bees for the presence of *Tarsonemus*. H. indicates that the stock from which the bees were obtained was showing no indications of disease, and was described by the owners as *Healthy*.

S. stands for *Sick* stock, and invariably indicates that the ordinary symptoms of Isle of Wight disease known to bee-keepers were present. The figures quoted under the heading *Tarsonemus* indicate the number of bees in which *Tarsonemus* was found.

TABLE I.

Ref. No.	Date.	Locality.	Condition of Stock.	Numbers Examined.	Tarsonemus.	Remarks.
1	22 May	Stonelhaven	H.	12	2	Developed the disease subsequently.
6	26 "	Edinburgh	H.	20	0	
7	"	Rubislaw	H.	2	1	No. 44 in record.
10	14 "	Aberdeen	S.	13	11	Requeened. Reduced to 1 frame, 30th October.
18	22 "	Kintore	S.	12	12	Crawling marked.
22	27 "	Northumberland	S.	5	5	Stock died out.
37	4 June	Copford	H.	31	0	Infected artificially later. Became queenless. Died out subsequently.
48	6 "	Shipton	H.	3	0	
57	8 "	Cults	H.	12	2	Died out from disease and queenlessness.
55	9 "	Bauchory	S.	3	3	
62	14 "	Kirriemuir	H.	9	0	
70	17 "	Huntly	H.	5	5	Early stage of infection. Disease very prevalent in immediate neighbourhood and robbing noticeable.
74	17 "	Glasgow	H.	34	3	No disease signs so far (30/12/20).
75	18 "	Drunlithie	S.	6	6	A stock dwindling from the disease. Minor tracheæ were blocked.
78	20 "	Cawdor	H.	30	0	(4 stocks.)
82	20 "	Aboyne	H.	6	6	Last stock of 6,—5 of which have already died of disease.
86	22 "	Laurencekirk	S.	20	17	An ordinary case.
92	21 "	Dingwall	H.	6	6	Stock much reduced and in bad condition, but no crawling had been seen.
94	21 "	Aberdour, Fife	H.	20	0	No record of disease in this apiary.

TABLE I.—*continued.*

Ref. No.	Date.	Locality.	Condition of Stock.	Numbers Examined.	Tars-nemus.	Remarks.
97 <sup>a</sup>	26 June	Bristol	S.	6	6	Heavily infected from a cast which up till a few days previously appear healthy. Crawling sudden and extensive.
99	28 "	Banchory	S.	6	6	An ordinary advanced case.
100	26 "	Rubislaw	H.	30	0	See record, No. 60.
102	29 "	Edinburgh	S.	13	10	Has shown none of usual signs of Isle of Wight disease, but has dwindled since spring. Queen found free of infection.
103	29 "	Northumberland	S.	12	12	
105	30 "	Turriff	S.?	7	5	Intermittent signs of disease shown. These bees not known to have the disease.
108	2 July	Ellon	S.	8	6	Reported 17th September:—"Now very healthy and closely packed down on ten standard frames. Gave one and a half crates shallow frames surplus."
111	2 "	Ellon	H.	13	0	Same apiary as No. 108.
112	2 "	Ellon	H.	7	1	Strong stock all along, swarmed twice. Gave two and a half crates shallow frames surplus. Never showed any signs of disease.
115	3 "	Port Elphinstone	H.	30	0	See record, Re No. 1.
116	3 "	Warrilow, Sussex	H.	7	0	
118	5 "	Cluny	S.	6	6	Intermittent disease history from previous September. Died out about this date.
119	5 "	Nairn	H.	5	0	
120	5 "	Cults	S.	13	13	An ordinary advanced case.
124	3 "	Inverurie	S.	6	6	Do.
126	8 "	Glasgow	H.	30	3	There have been no signs of the disease.
128	8 "	Keig	S.	6	6	
299	8 "	Witney, Oxon.	S.	6	6	Slight crawling only, at this stock.
129	8 "	Inverness	S.	6	6	Crawling observed for months previously. Infection very heavy.
134	8 "	Rubislaw	H.	30	5	Died subsequently of the disease.
140	9 "	Rubislaw	S.	19	19	From 4th June onward this stock by repeated examination (4 times in one month) showed practically every bee infected. It appeared to be doing moderately well. Mass crawling was never observed, but the stock became queenless and died out before the end of July.
141	10 "	Inverurie	S.	10	10	
146	11 "	Boat of Garten	H.	3	3	Stock believed healthy; from apiary where other four stocks had died from the disease.
148	13 "	Park	S.	4	4	Stock crawling. Drones were included in this examination.
149	14 "	Boat of Garten	H.	14	10	Not known to be sick, but some bees seem to have dislocated wings.
165	15 "	Coull	S.	5	5	Yielded a good top swarm, and crawling appeared subsequently. Tracheae were closely packed with mites in all cases.

TABLE I.—*continued.*

Ref. No.	Date.	Locality.	Condition of Stock.	Numbers Examined.	Tarso-nemus.	Remarks.
166	15 July	Rubislaw	H.	20	3	Infection slight. This stock died out in the course of the summer.
167	16 "	Rubislaw	H.	20	0	This stock later developed an infection. It is still in existence.
168	16 "	Dingwall	H.	8	8	
169	16 "	Italy	H.	22	0	Two samples. Attendants accompanying queens. Both lots infected with Nosema.
170	16 "	Bandon (Ireland)	H.	26	3	
153	11 "	Kinaldie	H.	7	7	Roof stock. All these bees were crawlers.
154	11 "	Kinaldie	H.	30	8	Same stock. All these bees were fliers.
175	18 "	Nairn	H.	11	0	
180	19 "	Rubislaw	H.	30	0	Standing in an apiary beside diseased stocks. It has since become infected, but there are no external indications.
190	21 "	Dorridge	S.	6	4	A strong stock of Italian hybrids with a 1919 queen.
191	21 "	Dorridge	H.	28	0	An Italian nucleus with a 1920 queen.
195	29 "	Fyvie	S.	7	7	Stock reported crawling for weeks previously.
199	6 Augt.	Norfolk	H.	12	3	Stock remains apparently healthy.
201	14 "	Norfolk	H.	3	2	A light infection.
202	14 "	Old Meldrum	S.	6	6	Died out from the disease.
216	18 "	Dingwall	S.	10	10	A bad case.
217	18 "	Birkenhead	H.	10	0	
219	20 "	Birkenhead	S.	10	10	From 2 stocks, examined separately; both infected.
222	20 "	Lucerne	H.	29	0	From 3 stocks.
230	26 "	Lugano	H.	44	0	From 2 stocks.
235	28 "	Wick	S.	10	10	A suspected stock. A definite case of infection in an area only recently affected by the disease.
239	30 "	Washington, U.S.A.	H.	37	0	
243	1 Sept.	Beaully	H.	9	0	
263	22 "	Bucksburn	S.	10	5	
264	23 "	Washington, U.S.A.	H.	23	0	
268	27 "	Eddieston	H.	21	0	Maintained in an area free from disease.
269	25 "	Weston-s.-Mare	S.	11	11	Two stocks; examined separately, both infected.
273	28 "	Austria	H.	20	0	
276	28 "	Stoke-under-Ham	H.	4	0	
277	28 "	Stoke-under-Ham	S.	4	4	Not known by owner to be sick, but crawling bees found.
283	17 Oct.	New Machar	H.	9	0	
287	17 "	New Machar	S.	10	10	Tracheæ badly blackened.
290	28 "	Rubislaw	H.	25	4	In infected apiary; no external signs of disease.
302	30 "	Bungay	H.	30	27	Some crawling about middle of month. Put up for winter.
303	30 "	Bungay	H.	28	23	No sign of crawling. Put up for winter.

TABLE II.

The following illustrates the progress of infection as observed in the periodic examination of 4 stocks of the same apiary :—

Date.	Locality.	Condition of Stock.	Number Examined.	Tarsonemus.
20 May	Fintry No. 1	H.	6	0
1 July	"	H.	3	1
3 Aug.	"	S.	7	7 Crawling bees.
"	"	S.	5	4 Fliers.
20 May	Fintry No. 2	H.	5	0 Fliers.
8 June	"	H.	8	2 Fliers.
3 Aug.	"	S.	4	4 Crawlers.
20 May	Fintry No. 3	H.	24	0 Fliers.
8 June	"	H.	16	1 Fliers.
1 July	"	S.	10	3 (8 fliers, 2 crawlers).
3 Aug.	"	S.	22	22 Crawlers.
20 May	Fintry No. 4	H.	15	0 Fliers.
3 Aug.	"	S.	6	6 Crawlers.

The data set forth in the foregoing Tables are thoroughly representative of our results as a whole. Examination of the figures quoted will show :—

1. That in every case of a "Sick" stock, *Tarsonemus* was present in the stock, and in a high proportion of cases it was found in every bee examined.
2. That in the majority of stocks marked "Healthy," *Tarsonemus* was not found.
3. That in a proportion (36 per cent.) of supposed "healthy" stocks, *Tarsonemus* was found. Of these within the period of observation (five months at most) a proportion eventually developed the usual symptoms, and died out from the disease. A proportion died out without having shown the symptom of "mass crawling," and a few remain apparently healthy.

Regarding the admittedly diseased stocks in which *Tarsonemus* has been found, we deem further illustration unnecessary. Concerning those other cases, some of which may appear to present difficulties, we consider it important that details should be submitted, and of these we now quote typical examples.

For ease of comparison the main facts regarding each are summarised at the end of the series.

## STOCK RECORDS.

*R. No. 1.*—This stock at the end of May was covering fully twenty frames and was in very good condition. On the 22nd of this month twelve bees taken entering the hive were examined for the presence of *Tarsonemus*. Two of the twelve were found affected at the initial stage. The parasites were few and the tracheæ were perfectly clean. As stated, there were no signs of disease. About a month afterwards the stock, which meantime had worked well and shown no signs of disease, was again examined. On this occasion fifty-two bees were searched, and of these forty-three contained the parasite. In most cases the tracheæ were heavily infected but the tubes were comparatively clean. A further sample was obtained upon the 6th July, and at this time twenty-five bees out of a total of twenty-eight taken were infected. It should be stated that these bees were taken at random by shaking off a frame into a box placed below. A number of these showed a bronzing of the tubes, especially at the forks. By this time the bees were showing some listlessness and not working so well. The owner made an artificial swarm, removing the old queen and supplying the main stock with a virgin Italian queen. Twenty-three pounds of drained honey were obtained at this time. The two stocks were subsequently placed side by side. On 21st July, in a sample of thirty-five bees, twenty-eight contained the parasite. About the third week of August, after a period of cold weather, crawling became evident in both stock and swarm. About the end of August a sample of twenty-eight bees was supplied from the parent stock, and of these twenty-six were badly parasitised. Both stocks continued to crawl in large numbers, and as robbing by other bees was going on, the owner destroyed them about the end of September.

*No. 44.*—This stock was obtained upon 11th April from an apiary which has been in existence for many years, and in which Isle of Wight disease has never been known. It was placed on the date mentioned in a new hive upon its own frames in an experimental apiary in which there were stocks suffering from Isle of Wight disease. The stock progressed normally throughout the summer and by the middle of June the bees were working in a super. On the 26th May an examination made on two bees taken from the stock showed one to be infected with *Tarsonemus*. Two days later one out of eight was found similarly affected. Subsequently, periodic examinations as follows were made on the dates mentioned.

Date.	No. Examined.	Result.	
		Infected.	Not Infected.
12 June	31	3	17
22 July	10	5	5
31 Aug.	33	32	1

Although during the whole of this period crawling symptoms never were in evidence and the bees appeared to be working normally, the numbers did not increase, nor were stores accumulated. In the later part of July and August the decline in numbers was rapid, and crawling developed towards the end. The stock was robbed actively and became extinct towards the middle of September. The apiary from which the stock was obtained remains clear of the disease.

No. 61.—On the 20th May a stock of Italian bees infected with *Nosema apis* was obtained from Glassel. It built up rapidly in the course of the following weeks and by the middle of July the bees were covering fifteen frames.

On the 30th May four bees were taken entering the doorway; these were active and inclined to sting; two of them were found infected with *Tarsonemus* and two were clear. On 7th July thirty bees were taken and of these five were infected. Again, on 14th July twenty bees were taken; ten were infected with *Tarsonemus* and ten were free. Up to this date there were no external signs of disease in the stock. The season being poor there were no surplus stores, but, as already stated, the stock was strong in bees.

On 30th August thirty-four bees were examined and of these twenty-seven were found infected, and about this date crawling amongst the bees was observed for the first time. By this date the stock was reduced to about seven frames of bees, and robbing by other bees was being persistently attempted. It eventually died out at the end of September.

No. A. Ch.—In the month of May a stock was obtained from an apiary in Dyce, where there had been no disease for many years. It was a swarm of the previous year, and after transference was isolated from other stocks. On 17th July six bees taken from the stock, which appeared perfectly healthy, were all found infected, but to a slight degree. The infection appeared to be recent. A fortnight later crawling became evident in the stock, and six crawling bees supplied were found to be all infected and more extensively than in the previous sample. By the 1st September the stock had declined to about four frames of bees. There were no stores. Nine flying bees were taken; these were all found infected and having their tracheal tubes much blackened. The owner at this date destroyed the bees.

No. Glasgow, I.—On the 8th July a sample of thirty bees was taken from a stock of Dutch bees obtained from West of Scotland College of Agriculture on 22nd March. The stock at the time the sample was taken appeared perfectly healthy and was doing well. Of the thirty bees, three were found infected with *Tarsonemus*. The stock swarmed, and the swarm for a time appeared strong and healthy. At the beginning of August the parent stock covered eight frames, with stores and brood on six. No loiterers or crawlers have been observed at either the parent or swarm stocks. Thirty-five bees of the parent stock were examined at this date, and of these three were found infected with *Tarsonemus*.

It remained so at the end of October, although at this date it showed a proportion of infected bees of about 27 per cent. (33 bees, 9 infected).

At the present time (30th October) this stock is strong in numbers, without visible signs of disease. The owner has united it with one half of the swarm.

*No. Glasgow, P.*—This stock at the beginning of June was strong and working well. The bees covered ten frames, six of which were very well filled with brood. Brood was also present upon the other four and there were plenty of stores. The stock swarmed at this date but the swarm, secured with difficulty and with a loss of bees, was returned to the parent stock. On 17th June a sample of thirty-four bees was examined, and of these three were found infected with *Tarsonemus*. There were no external signs of disease and matters appeared normal with the stock. During the next three months the owner paid little attention to it, and in September the bees were reduced to four frames with brood and were without food. None of the usual signs of Isle of Wight disease had ever been seen about the stock, which was now being fed. A sample of twenty-nine bees was taken on 7th September, and of these two only were infected. This shows a slight decrease as judged by the samples. A later sample supplied at the end of October, however, showed an increase in proportion of infected bees. The stock as a whole does not appear affected by the presence of the parasite, but it is not particularly strong in numbers.

*No. 62.*—Early in May of this year a nucleus of three frames of bees with queen and brood was obtained.

On 27th May fifteen bees, and again on 3rd June four bees, were examined for *Tarsonemus*, with a negative result. The bees were standing in an infected apiary and at this time were working well and rapidly increasing in numbers.

On 14th June twenty-five bees were examined, and of these twenty-two were found clear of the parasite; of the remaining three, two contained several parasites and one a single adult female. The bees multiplied rapidly and swarmed twice in the course of the summer.

On 15th September thirty-three bees were examined, and of these nineteen proved infected.

At this date there were no signs of disease as far as behaviour of the bees was concerned. The numbers were well maintained and the stores sufficient.

At the end of October, forty bees were taken and all except three were found infected. The pathological features were not marked. The stock is apparently in a strong condition as regards numbers at this date.

*No. 60.*—On 20th May a small lot of bees covering three frames was obtained, which on examination was found to be harbouring the parasite *Nosema apis*. Apart from this there were no external signs of disease about the stock, and it built up moderately well. By 2nd August the bees covered over nine frames, with brood upon seven. The season was poor and stores were short.

At the middle of September the stock appeared well, apart from a shortage of stores. Further at this date *Nosema* was still present.

In the course of the summer, bees of this stock were periodically examined between 17th June and 27th September for the presence of *Tarsonemus*. In all one hundred and fifty-six bees were tested and on only two occasions, namely upon 20th August and 27th September, was *Tarsonemus* found. In each case only one bee was found infected. This and a preceding stock (No. 61) were obtained from the same apiary and have stood together, but a little way apart from the other stocks, during the period of observation. Several of these other stocks in the same apiary were at this time suffering from Isle of Wight disease. At the end of October a sample of thirty-five bees was taken off the frames, and all were found free from *Tarsonemus*.

*W. No. 2.*—This stock, on 4th August, headed by a young queen, appeared normal and in good condition. There were no visible grounds for suspecting infection. Of twelve bees taken at this date, three were found harbouring *Tarsonemus*.

On 6th September the bees were covering most of the frames, and there was a good amount of sealed brood and eggs in the inner frames. There were no signs of disease. At 20th September one crate of sections honey was obtained and about 20 lbs. of stores were left in the hive. At this date fourteen bees were taken at random, and of these twelve showed infection with *Tarsonemus* and two were clear.

At the end of October, of twenty-eight bees supplied, twenty-three were found infected.

*No. 24.*—This was a nucleus of five frames of Italian bees obtained upon 11th June.

Twenty-two bees were examined at this date and these were found to be free from *Tarsonemus* infection. A fortnight later thirty-two bees were examined and one bee only was found containing this parasite; everything appeared normal with the stock. Throughout the summer the stock prospered only moderately well. In the first week of September twenty-three bees were taken at random, and of these one only contained *Tarsonemus*. The stock has yielded no surplus stores and there has been no indications of disease. *Nosema apis* is not present in the stock and the apparent weakness cannot be attributed to it or to *Tarsonemus*.

Twenty-two bees were examined, and all found negative, on 29th October 1920. It would, therefore, appear that although *Tarsonemus* was present in the stock as early as the 25th June, there was no apparent increase in the incidence of infection as late as the end of October.

*Re. No. 1.*—This stock was brought to Aberdeenshire in the month of June from Caithness-shire. The bees, headed by a 1919 queen, were bred in this district in an apiary which had existed for many years and has had no experience of the disease. Thirty bees were examined on 3rd July and all were found free from *Tarsonemus* infection. The bees were placed in an area which has not been free

from Isle of Wight disease for a long time. On the 9th September the owner reported "so far the bees have done well and the stock is strong, but I have made no attempt to take honey; indeed, I have been feeding a little recently just to keep the queen breeding so as to supply young bees for winter."

At this date a second sample, consisting of twenty-two bees, was supplied, and of these, one bee was found harbouring *Tarsonemus*. The infection was localised just inside the spiracle of one side, and was limited to one adult and a few ova.

It is practically certain that infection of the stock in this case was effected within three months and probably not much earlier. In other words the stock stood in a highly infectious area for over two months without contracting the disease.

At the end of October, the owner reported the stock as "specially strong." A sample of six bees was received, and of these, one was found harbouring *Tarsonemus*, the other five being free.

*Re. No. 2.*—A second stock of similar origin, and with queen of same age, was obtained and placed alongside No. 1, just described, upon the 9th July. Exactly two months afterwards a sample of fifteen bees was taken and found free from infection. The stock is strong and is receiving similar treatment to the other.

Of a sample of twenty-one bees of this stock examined at the end of October, twenty were free from infection and one showed an initial infection, consisting of a few mites near the spiracle on one side. The owner reported it as "lively, and taking in pollen. There have been no signs of crawling about this hive. There is plenty disease in the neighbourhood."

*R. No. 2.*—Early in August a presumed healthy stock of bees was placed alongside two stocks both at the crawling stage of Isle of Wight disease. At the end of August thirteen bees were taken from amongst the foragers as they entered the hive. Ten were clear of parasites and the remaining three were affected, all of them slightly. Two of the infected cases showed only one or two adults and a few ova just within the spiracle of one side. Infection had evidently taken place during the period the stock was upon this site and not before. Upon advice given, the stock was removed at the end of August some distance from the others referred to above. At the end of October the owner reported: "It has filled up fairly well on the heather, is very lively and seems all right. To-day they are gathering in pollen and I send you a sample from those that were flying out and in."

The sample contained thirty bees, and of these twenty-nine were infected with *Tarsonemus*. There was a fair amount of bronzing of the tracheæ, all stages of development were present, and in a number of cases the mites were densely packed in the outer tubes.

*W. No. 3.*—This stock, requeened in the middle of July, was normal and in good condition on 14th August, when, out of a small sample of three bees, two were found to be infected. On the 6th September the stock was examined and found to have bees covering nearly ten frames, with plenty brood and eggs. This stock has

yielded four crates of sections and had fifteen pounds of stores left in the hive. The owner writes, "I am pleased to state there are no signs of any trouble." Seven bees were supplied from the stock, and of these five were harbouring *Tarsonemus* at the same date.

About the middle of October a slight amount of crawling was observed in this stock, but weather conditions have prevented further observations. At the end of October a sample of bees supplied was found heavily infected. The stock continues under observation.

#### NOTES ON STOCK RECORDS.

*R. No. 1.*—In about six weeks after the infection was first discovered, but not until the incidence of infection had risen to over 89 per cent., did visible signs of the presence of the disease appear.

*No. 44.*—This stock certainly developed an infection of *Tarsonemus* within the period of 11th April to 26th May, *i.e.* about six weeks. The examinations showed a rapid spread of *Tarsonemus* within the colony, so that in a little over four months from the arrival of the stock the incidence of infection was 97 per cent. And yet crawling was never in evidence until near the end.

*No. 61.*—This stock shows a striking parallel to the previous. Within the three months from 30th May to 30th August, the infection rose to about 80 per cent., and only now did crawling symptoms appear, although meantime the stock had visibly declined in numbers.

*No. A. Ch.*—Examination of bees from the original apiary in September, which were showing suspicious signs, showed that they too were infected with *Tarsonemus*. It appears probable that this stock was infected before leaving the original apiary, and from the fact that on 17th July the percentage of infection was so very high it would appear that the distribution of *Tarsonemus* was well established, though probably of recent origin.

*Glasgow, I.*—This stock was known to have a definite infection on the 8th July, which rose at the end of October to 27 per cent., without disease signs appearing. This is a case in which the spread of the disease within the stock is progressing with relative slowness.

*Glasgow, P.*—This is a similar case to the foregoing in that the spread of infection has been slow, and in which the ordinary disease symptoms have never appeared.

*No. 62.*—Nearly six weeks in an infected apiary elapsed before this clean stock was found to be harbouring *Tarsonemus*. After four and a half months from the time the presence of *Tarsonemus* was first discovered the incidence had increased to over 92 per cent., and no disease symptoms have ever been seen and the stock appears in a prosperous condition.

*No. 60.*—This is a stock which, although found to have *Tarsonemus* present in August, appears to have lost the infection.

*W. No. 2.*—*Tarsonemus* has been known to be present in this stock since the beginning of August. It is now wintering, and no signs of disease have ever been observed.

*No. 24.*—Infection from near the end of June to the beginning of September and not found later. Stock has not prospered.

*Re. No. 1.*—Slow progress of infection. No signs of disease; stock wintering.

*Re. No. 2.*—Infection took place within three months, and the progress very slow.

*R. No. 2.*—Proximity to two heavily infected stocks is a feature of this case. Infection probable within a month, rose in two months about 97 per cent., and the stock has dwindled to very small dimensions.

*W. No. 3.*—Known to be infected for two months before any suspicious signs appeared, and these only slight in character. The stock has done well, but its possible survival till spring is doubtful.

TABLE III.

Date.	Locality.	Condition of Stock.	Numbers Examined.	Tarsonemus.	Remarks.
24 Sept. 1916	Aberdeen	S.	5	4	Crawling bees.
24 Apr. 1917	Rubislaw	S.	1	1	Development stages of parasite.
26 " 1917	Glassel	S.	9	8	Stock crawling.
5 July 1917	Aberdeen	S.	1	1	All stages of development of parasite.
1 Feb. 1918	Stoneywood	S.	3	3	" "
18 July 1918	Glassel	S.	1	1	" "
11 Jan. 1919	Aberdeen	S.	7	7	" "
8 Dec. 1919	Aberdeen	S.	3	3	Stock crawling.

The bees referred to in the foregoing table were all obtained from stocks recognised as suffering from the disease. The bees had been preserved on the dates mentioned. The results confirm the presence of *Tarsonemus* in diseased bees over the four years 1916–20, and also make clear the important fact borne out by the 1920 examinations that the breeding of *Tarsonemus* goes on throughout the whole year.

## GENERAL CONSIDERATIONS.

For a sound appreciation of the foregoing records, and particularly of their diversity in detail, it is necessary that the various factors likely to be present affecting the course and culmination of the epizootic within the bee colony should be clearly set forth.

A colony of bees consists normally of a population which particularly in summer is undergoing a continuous and relatively rapid change, both as regards its constituent members and also as regards the total numbers. Daily during the working season there is both a steady mortality and a steady increase. This latter depends

upon the age and fertility of the queen. Also, for normal prosperity, there must be maintained a definite proportion of nurse bees and foragers.

In a colony affected with disease of any kind, which significantly affects the normal mortality rate, the age incidence of the mortality amongst the workers, and the productivity of the queen, are characters of the highest importance as affecting the maintenance of the colony as an effective and prosperous unit. These two opposing factors struggle with each other—losses from idleness and crawling, and mortality due to disease, added to the normal wastage on the one hand, and gains from the production of new bees on the other. A young and prolific queen by sheer production of new bees may so keep down the proportion of infected and hence more or less ineffective members as to render such a colony to some degree profitable.

Disease may be maintained within a colony in two important ways. It may be instituted by the infection of a few members of the colony by contact with a single bee carrying mites, which has mingled in the cluster. This may be a stray bee from another colony or a member of the stock which has been robbing a diseased colony, and such infection may constitute the only one from the outside. In this case we may expect that progress will be slow, if indeed the infection does not die out. The attacked bees may be old and die away from the hive before transmitting *Tarsonemus* to other members of the colony, or the infection may be so swamped by normal increase as to be practically ineffective. Whether a stock once infected is doomed sooner or later in every instance we have not sufficient evidence as yet to say. Some of the cases quoted, if the samples of bees taken may be regarded as representative, appear to have lost the infection. And we do have some evidence that extinction may be delayed for a long time. RENNIE and HARVEY, No. 1 (1919), have already directed attention to cases where the source and time of infection of a stock was known in autumn and the usual symptoms did not become evident until the following year.

A second and highly important factor, however, which we are satisfied is very frequently in operation, is repeated or multiple infections continued from the outside over a considerable period of time. We then have the disease spreading from many foci. The drifting of bees into strange hives is common. Once the disease has gained some ground, the social instinct of the colony is weakened, both by the disturbance of the normal balance of worker types and by the illness of a high proportion of bees. Robbing may now take place, and amongst the robbers there may be infected bees which will intensify the trouble. This robbing, at first resisted, is eventually allowed to become rife, and when this is established we have noticed that extinction is practically inevitable.

Other factors which may tell against the stock are the presence of an indifferent queen whose production may be poor, and from whose low racial vigour shorter-lived bees result.

The varying character of the factors shows that a uniform course of spreading of

infection within a stock is not likely to occur. Yet apart from any special combination of adverse factors, it appears to be common for the disease to steadily gain ground within a stock once it is established. It is, however, clear that no sound argument against the view that *Tarsonemus* is the cause can be built up from cases where, in the presence of *Tarsonemus*, disease did not spread within the stock and destroy it as a whole, so long as it can be shown that there is an associated pathology which in due course renders the infected bees ineffective members of the colony, and all the time causes loss of bees by crawling or directly by death.

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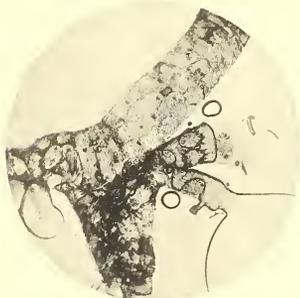
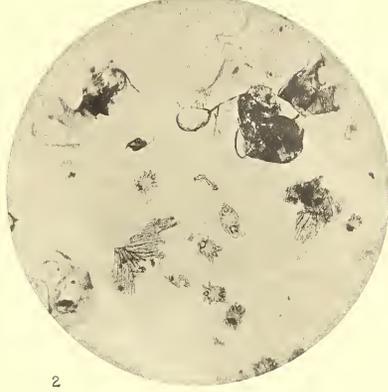
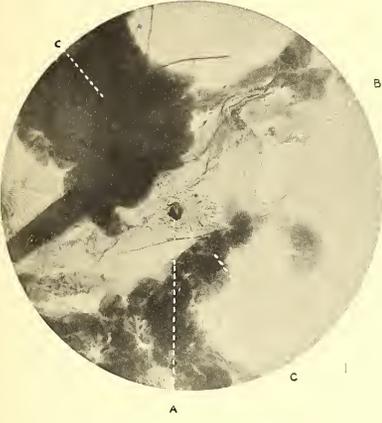
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#### EXPLANATION OF FIGURES.

All the figures are photographed with Watson Service Microscope.

- Fig. 1. *Tarsonemus* in trachea of hive bee. The first specimen observed. A. *Tarsonemus*. B. trachea. C. thoracic glands.  $\frac{1}{2}$  in. oil imm. obj., ocular No. 2.
- Fig. 2. Teased preparation of infected trachea showing various stages of *Tarsonemus*.  $\frac{2}{3}$  in. obj., ocular No. 2.
- Figs. 3, 4, and 5. Tracheæ containing *Tarsonemus*.
- Fig. 3 shows the blackening of the tubes.
- Fig. 5 shows blocking of wider tube with larval stages.  $\frac{1}{8}$  in. obj., ocular No. 4.
- Fig. 5, ocular No. 4.
- Fig. 6. Section of infested trachea wall. A. not badly affected. Mites seen in section.  $\frac{1}{8}$  in. obj., ocular No. 4.
- Fig. 7. Do., showing A. thickening of wall of tube. B. Two ovigerous females *in situ*.  $\frac{1}{8}$  in. obj., ocular No. 2.

RENNIE, WHITE, AND HARVEY: ETIOLOGY OF ISLE OF WIGHT DISEASE.





XXIX.

- (2) **The Pathology of Isle of Wight Disease in Hive Bees.** By P. Bruce White, B.Sc., Bacteriologist to the Bee Disease Investigation, University of Aberdeen and N. of Scotland College of Agriculture. *Communicated by* Dr JOHN RENNIE. (With One Plate.)

*(From the Department of Pathology, Marischal College, Aberdeen.)*

(Read November 1, 1920. MS. received December 7, 1920. Issued separately March 25, 1921.)

Isle of Wight disease is, as we have seen, primarily a disease of the respiratory system, in which the organism remains localised throughout the entire course of the attack.

The effects are, however, far-reaching, and are registered in the disordered functioning of several organs, and in visible pathological changes in some of them.

The parasitic invasion has two aspects.

We have, in the first place, to consider the active injury wrought upon the host by a parasite developing and living at the expense of its body fluids. With this aspect of the question may be coupled the possibility of a definite toxic action on the part of the parasite.

In the second place, we have to consider the passive rôle of the mites in hindering or inhibiting the normal functions of the infected organs.

Before proceeding to consider the various pathological conditions, a few words on the distribution of the parasite within the host is called for.

In infected bees the mites are consistently present in the tracheal system of the thorax, and in a certain number of bees are also to be found in the air-vessels of the head. No mites have, up to the present, been discovered in the abdominal system.

The primary parasitic invasion takes place through one or both of the first pair of spiracular orifices, and apparently through these alone. The whole anterior thoracic system of major tracheæ and air-sacs is liable to infection. The infection may be unilateral or bilateral, and in some cases where the mites have entered on one side only, they may migrate into the vessels of the other side, setting up a secondary bilateral infection. The passage is effected through the roots of the anterior air-sacs, which form a commissure between the large paired vessels supplying the head.

A single mite may enter the bee, or several may enter together or at intervals. Sometimes the pregnant female may advance as far as the secondary tracheæ before depositing eggs, but the primary trachea becomes involved sooner or later in the vast majority of cases.

It is usually only in the later stages of the attack that the mites attain the smaller tracheæ, the thoracic air-sacs, and the vessels of the head. In such cases,

however, the young mites frequently advance as far as the calibre of the vessels permits.

The various pathological conditions which may be encountered in infected bees will now be considered, the various systems being treated of in sequence.

#### TRACHEAL SYSTEM.

*Macroscopical appearances.*—The first change visible to the naked eye is an increased opacity of the infected vessels due to the aggregation of ova and the younger forms of the parasite within the lumina. As the disease advances the trachea assumes a brown tint, which gradually deepens and becomes flecked with black. Finally considerable portions of the infected tracheæ may become dead black. This change in colour is accompanied by an increasing hardness and brittleness of the parts, which become rigid. This brittleness results in a phenomenon which is of some use in the field diagnosis of the disease. It is frequently found that upon exerting moderate pressure upon the upper surface of the thorax of bees crawling from the disease, that a drop of fluid—blood—will exude from the first spiracle of one or both sides, the rupture of the trachea at its insertion having thrown the hæmocœle open to the exterior.

*Microscopic appearances.*—During the earlier stages of the attack, the oval and almost colourless ova and embryos may be seen lying within the lumina of the tracheæ. The parent mites, too, may often be found in the vicinity. The tracheal wall may show here and there a few fragments of brownish matter, the fæces of the invading adults.

This condition is maintained till, with the appearance of the later developmental stages of the parasite and the young adults, the wall becomes encrusted with granules of fæcal matter. These granules, irregular in size and discoid or spherical in shape, become arranged in the interspaces between the tracheal thickenings, forming an irregular series of transverse bands upon the tracheal wall. They are of a brownish or yellowish colour, and when densely aggregated appear black. The colour of the deposit upon the wall therefore varies with the thickness of the crust and the amount of pigment it contains. The pigment may become extracted, leaving the pallid granules behind.

A similar deposit may collect in the lacunæ between the parasites themselves.

A typically affected tracheal tube is shown in fig. 1, while a fragment of the encrusted wall is shown further enlarged in fig. 2.

The fæcal matter may, further, be inhaled and, though the bulk appears to be trapped in the air-sacs and larger vessels, may attain the finer ramifications of the system, sometimes forming small emboli in the tracheoles. This is particularly frequent when the parasites are present in the air-sacs.

Careful study of the tracheal wall for perforations reveals little. In two cases

only has it been possible to observe the long piercing apparatus of the mite actually passing through punctures in the wall. The material damage done in this way is seemingly small.

#### MUSCULAR SYSTEM.

Visible pathological changes of the muscle fibres occur, but these are apparently restricted to the thoracic muscles of flight. Though a considerable number of fibres, in highly infected crawling bees, may show signs of the atrophic change to be described, the number showing definite degenerative changes is usually small. While no such changes have been noted in non-infected bees of whatever age, they may occur in infected bees which show no outward symptoms of the malady. On the other hand, a percentage of infected crawling bees show no marked muscle changes.

*Macroscopic appearances.*—Upon teasing out in saline the thoracic muscle mass of a bee crawling from the disease it is usually found that certain fibres—averaging 2-6 in number—contrast markedly with the flaccid, greyish-yellow normal fibres by their opaque white colour, slenderness, brittleness, and rigidity.

*Microscopic appearances.*—Under the low power of the microscope these white fibres are conspicuous by their slenderness, density, and granular appearance. The ends show an irregular fracture quite unlike the frayed-out ends of the normal fibres. A number of micrometer measurements on these and on healthy fibres of the muscles of flight gave the following values:—

Average width of healthy fibres of muscles of flight =	.24 mm.
" " atrophied " " " =	.12 mm.

In fresh preparations examined with the 1/6" objective it was possible to make out the nature of the change which had taken place.

In the normal muscle of the bee the bulk of the fibre is composed of the fibrillæ, upon and between which lie the large flattened sarcosomes or myochondria. These granules mask the transverse, but not the longitudinal, striation of the fibre. When the fibre is teased out the fibrillæ fray out, allowing the diaphanous sarcosomes to escape.

In the case of the atrophied fibres of infected bees the appearances are different. Microscopic examination may show little or nothing of the original fibrillar structure. It is often found that the bulk of the fibre is composed of densely arranged longitudinal columns of closely packed and very coherent sarcosomes which do not escape and float away when the fibre is teased out. Between these granular columns, it is found, upon closer examination, that remnants of the fibrillæ persist, though many may be reduced to thread-like vestiges of their original form.

A drawing of the low-power appearances of normal and atrophied fibres is shown in fig. 3, and a piece of atrophied fibre is drawn under the high power in fig. 4,

while in fig. 5 the substance of a highly atrophied fibre (A) is contrasted with two normal fibrillæ and normal sarcosomes (B).

The sarcosomes of the atrophied fibre are much denser and more cubical in shape than the normal granules, and may be of relatively enormous size. In highly degenerate fibres they may form conglomerate masses of considerable size.

When degenerate muscle is treated with dilute acetic acid the fibrillar vestiges swell, forcing the granular columns apart, and a picture closely resembling normal muscle when treated in the same way is achieved.

When freshly obtained normal and atrophied fibres are placed in a drop of dilute eosin or methylene blue, it is found that while the former are only slowly and superficially stained, the latter become rapidly and deeply stained through their entire substance. This would seem to indicate that the degenerate fibres are dead.

Though various fixation and staining methods have been employed, they have added little to the facts derived from the study of fresh material.

These muscle changes may be summarised as—

A general wastage of the fibrillar substance and loss of sarcous fluid, with the condensation of the frequently enlarged sarcosomes in densely arranged longitudinal columns, the process resulting in a shrinkage of the fibre with loss of function.

All stages in this process are, of course, to be encountered.

A further feature of some atrophied fibres, and occasionally of those which do not show the typical signs of wastage, is the development of pigmented spots in their substance. Such spots are represented in fig. 5.

These spots vary in colour from yellow to a deep brown or black, and often appear to bear a definite relationship to the distribution of the tracheoles supplying the muscles.

Careful scrutiny has not entirely elucidated their origin. It seems possible that they may be caused by staining of the muscle by the fæcal dye of the parasite, which has percolated into the final ramifications of the tracheal system.

Other explanations which have been considered are that the discoloration is due to a degenerative process in the muscle or to an accumulation of waste products. This point may perhaps be cleared up by further work.

In some diseased stocks these spots are found in almost every crawling bee; in others, apparently at the same stage of the disease, they are absent.

#### THE BLOOD.

The blood of the crawling bee is often scanty, though when such bees are warmed and fed they recover their normal complement of body fluid.

No qualitative cytological difference has been noted between the blood of healthy and crawling bees, though the number of cells per unit volume may be increased in the latter. This increase is probably entirely due to loss of plasma and cannot be regarded as a leucocytosis.

## THE ALIMENTARY SYSTEM.

As regards the alimentary system, the investigation has but little to add to the observations of former workers. The disordered condition of the alimentary tract has attracted much attention in the search for a clue to the causation of Isle of Wight disease.

The facts may be briefly outlined.

In the majority of crawling bees the hind gut and small intestine are distended to the limit of their capacity with accumulated fæces, and the contents of the lower region of the chyle stomach may contain a large admixture of fæcal matter. The chyle stomach itself may present a rather wasted appearance, and its contents may be of an unusually deep purple colour. These changes are in all probability merely due to a reduction in the fluid contents of the organ.

In the vast majority of crawling bees no lesion is to be found in the alimentary wall either macroscopically or in stained sections. On two occasions only have signs of penetration of the wall by organisms (other than *Nosema*) been noted. In one case there was an infiltration of the wall near the insertion of the Malpighian tubules by a large filamentous bacillus; in the other case fungal hyphæ had invaded the epithelium of the lower portion of the chyle stomach. Such phenomena are to be regarded merely as terminal infections.

The flora of the alimentary tract of the normal bee has been carefully investigated and compared with that of bees crawling from the disease. Very little qualitative difference has been found between the two.

In Isle of Wight disease there is a colonisation of the chyle stomach by the intestinal organisms, and certain organisms, such as coliform bacilli and yeasts, are more frequent and abundant than in healthy bees. Certain streptococci, to be described elsewhere, have also a predilection for the alimentary tract of Isle of Wight bees.

## MALPIGHIAN TUBULES.

In a proportion of crawling bees certain of the Malpighian tubules, when mounted in saline, may possess a bright yellow colour due to the presence of large amounts of the excretory pigment. In these coloured areas the excretory granules within the epithelium may be abnormally large and spicular. In fresh preparations the cells appear to be filled with large bacilli. A similar condition may arise in bees after a period of confinement.

## NERVOUS SYSTEM.

The examination of the nervous system for pathological changes is as yet very incomplete. The observations of the writer have been mainly restricted to the thoracic ganglia. No changes have been noted in the posterior thoracic ganglionic

mass, and the few sections which have been examined of the anterior thoracic ganglia of sick and healthy bees show no alterations which cannot be accounted for as physiological variations due to senility.

#### DISCUSSION.

With these facts before us an attempt may be made to discuss the correlation between the action of the parasite, the pathological changes, and the symptomatology of the disease.

We have alluded to the two aspects of the primary effect of the parasite upon the host: the active injury produced by a parasite living upon the host fluids, with the added probability of a toxic action, and the passive obstruction of the respiratory system of the head and anterior thorax.

The pregnant parasites producing many, relatively large ova, the developing brood and the young adults must make considerable demands upon the host. It has been pointed out that the blood of crawling bees is often scanty, but it is improbable that this is in any significant degree directly due to the mites, but arises from the fact that fluid lost by excretion and transpiration is not replaced owing to the inability of the stricken bee to take or to obtain food. As many heavily infected bees continue to forage, though their tracheæ are bronzed and blackened by long sojourn of the mites, it would seem probable that nutritive sapping does not *per se* render the bee effete.

The same uncertainty surrounds the question of a toxic action. One member at least (*T. intectus*) of the genus to which the parasite belongs is known to be venomous, but the exact importance of this factor in the disease must, like the foregoing, remain for the present a matter of surmise.

The passive action of the parasites and their products in partially or completely blocking the infected tracheæ is a factor of which the importance is much more readily estimated.

It is obvious that any obstruction of the tracheal lumen must reduce the efficiency of the respiratory exchange of the organs supplied. In the vast majority of crawling bees the effective lumina of certain of the major tracheæ are obviously very much reduced, and in some all but obliterated. The organs supplied by such tracheæ must be reduced to an acute degree of oxygen starvation, and among the organs of which the respiratory supply is thus endangered are those of the head and the thoracic muscles of flight.

It is clear that the effects must vary from case to case:—

- (a) With the degree of the obstruction.
- (b) With the position of the obstruction.
- (c) According as to whether the obstruction is bilateral or unilateral.

The actual number of parasites distributed through the respiratory system is from

this point of view of secondary importance, a fact which may explain the apparent vigour of many heavily infected bees.

In order to obtain some idea of the effects actually arising from mechanical obstruction of the spiracles, a series of experiments were undertaken upon healthy bees. In these experiments melted paraffin wax was applied to the first spiracle of one or both sides of each bee in such a way as to give, on solidification of the wax, complete closure of the spiracular orifice without impairing the free play of the wings.

Bees treated in this way were maintained in boxes and were examined at intervals. In each experiment ten to twenty experimental bees were employed, and parallel controls were kept under the same conditions.

Upon closure of one spiracle the experimental bees at once lost the power of flight, but remained otherwise active in their movements, running quickly over the bench and beating the air with their wings. Upon the second and third days it was sometimes found that a proportion of the bees were capable of flight—which was, however, usually of very short duration. In these it is probable that the wax had become partially dislodged. The majority of the bees continued to crawl. After the lapse of several days these crawling bees became more sluggish in their movements, sometimes showing a tendency to drag their hind legs, and about the sixth to seventh day, bees were noted which showed a dislocation of the wings similar to that so common among bees crawling from Isle of Wight disease. About this time, too, some of the bees began to die: many were, however, maintained up to the beginning of the third week. During this period also a few of the control bees died, but the remainder retained the power of flight throughout.

At intervals experimental and control bees were killed for examination. Both in the “artificial crawlers” and in those control bees which had not been given opportunity to void their fæces on the wing, the hind gut was found distended with fæcal matter. At the end of the first week of experiment it was found that the thoracic musculature of the experimental bees showed, in many cases, atrophy of exactly the same type as had been found in infected bees. The degree of this atrophy and the number of fibres affected varied with the duration of the experiment. No such changes were noted in the control bees.

In those experiments in which the first spiracles of each side were closed with wax, the phenomena were different. As before, the power of flight was at once lost, but after twenty-four to forty-eight hours the bees had developed a reeling gait and appeared to be continually falling over their own heads. It was seldom that any survived the third day. No muscle atrophy was to be discovered, death having supervened too rapidly for the accomplishment of this change.

From these experiments it may be stated that:—

Through closure of the first spiracle of one side, a condition of crawling is induced which bears a close resemblance in its symptoms to Isle of Wight disease, and that,

further, the procedure may occasion atrophic muscle changes which are only known to occur in that disease. When the first pair of spiracles is closed, a state of complete incapacitation results, ending rapidly in death.

Though too close a parallel must not be drawn with the natural disease, these experiments are illuminating in that they give a basis to the view that the rôle of parasites in partially preventing thoracic respiration is of prime importance in the disease—possibly in itself capable of occasioning all the symptoms by which we are wont to diagnose the disease and the muscle atrophy so often associated with it.

The pathological syndrome of Isle of Wight disease is undoubtedly complex. Apart from the sapping of the host fluids and the probable injection of a venom, the mites may impair the mechanism of the bee either by destroying the respiratory supply of the individual organs or by cutting off that of the nerve centres which control and co-ordinate their activities. It is possible that the indirect effect through the nervous system, possessed as this is of a dual respiratory supply, is particularly acute when there is considerable bilateral obstruction of the tracheal system.

Through the combined influence of these factors the power of flight is lost, and a series of secondary conditions arise.

The fæces normally voided on the wing accumulate, thus increasing the difficulty of locomotion and compressing the abdominal air-sacs—another blow at the respiratory function. Intestinal pressure must hinder the excretory activities of the Malpighian tubules, and this excretory stasis, together with the absorption of toxins from the stagnant gut, must be reflected back upon the body of the insect.

As soon as the power of flight is lost death of the bee becomes imminent, for once it leaves the warmth and stores of the hive, unable to return, it perishes of cold and starvation. Should it elect to remain within the hive it is faced with a prospect of functional stagnation which cannot be indefinitely maintained. It would seem too that in the colder months sick stocks often perish *en masse* through inability to maintain the hive temperature.

It seems that in rare cases individual bees may recover from the attack upon being abandoned by the parasitic brood. Such cases are recognised by their bronzed and blackened tracheæ, which, however, contain no living mites. Bees in this condition have been found foraging for infected stocks.

#### CONCLUDING REMARKS.

It is somewhat remarkable that the macroscopic changes of the thoracic tracheæ and muscle have so long escaped observation in spite of the detailed examinations of several independent workers.

IMMS (1) held that "the disease is eminently one of the digestive system, and might be described as a condition of enlargement of the hind intestine," while

MALDEN (2) was of opinion that "the disease must be regarded as an infectious one which primarily affects the chyle stomach."

The latter states that in his investigations "no changes were discovered in the salivary glands, brain, fat body, *tracheæ*, *air-sacs*, Malpighian bodies, or honey stomach," but that "the chyle stomach in many cases showed marked changes in section." Of these changes in the chyle stomach the present investigation has seen little or nothing. Two exceptional cases have been noted where the epithelial lining had been definitely invaded.

MALDEN, as a result of his bacteriological work, suggested a "plague-like" bacillus, called by him *B. pestiformis apis*, as the cause of the malady. He, however, made the suggestion with some reserve, and later, when his work had been overshadowed by the "Nosema theory," considered that toxins produced by various species of bacteria played an important secondary rôle in the disease.

There is, however, an underlying truth in his summing up: "The actual cause of death is uncertain, but it is probably brought about by malnutrition, possibly combined with the absorption of a specific poison and of the products of decomposition in the colon, and probably aided to some extent by the imperfect oxygenation of the tissues, owing to the pressure exerted by the distended colon on the abdominal *air-sacs*."

Imperfect oxygenation, and possibly malnutrition and a toxic condition, are the main factors in the disease as we see them to-day.

In this paper it has been sought to outline those pathological facts which have so far come to light, and to relate them as reasonably as possible to the action of the parasite on the one hand and the symptoms of the disease on the other. Certain points have been merely touched on and others left in doubt, but it is hoped that further details will be soon forthcoming.

There are many to whom my thanks are due. To Dr J. RENNIE, who, as director of the research, has been an inspiring leader throughout, I tender my warmest thanks for help and advice and much personal kindness. My sincere thanks are due to Professor T. SHENNAN and the staff of the Pathology Department, Marischal College, Aberdeen, who have given me every facility for carrying out this work. It was in the Pathology Department that the parasite was independently discovered on the 11th May 1920, and the theory of its significance in the disease formulated. I wish also to express my gratitude to Professor J. ARTHUR THOMSON, Mr A. H. E. Wood, and the members of the Joint Committee of the University of Aberdeen and N. of Scotland College of Agriculture for all their interest and support.

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#### REFERENCES TO LITERATURE.

- (1) LINDS, *J. Board of Agric.*, vol. xiv, No. 3, June 1907.
- (2) MALDEN, *Ibid.*, vol. xv, No. 11, February 1909.

## DESCRIPTION OF FIGURES.

Fig. 1. Infected trachea showing typical changes. The black faecal deposit is arranged in transverse lines. ( $\times 70$ .)

Fig. 2. Fragment of wall of infected trachea, shown much enlarged. Granular deposits of faecal matter lie between the tracheal thickenings.

Fig. 3. Normal (*n*) and atrophied (*a*) fibres from the thoracic muscle of a crawling bee. Note the density, slenderness, and fractured ends of the atrophied fibres. ( $\times 50$ .)

Fig. 4. Fragment of an atrophied muscle fibre showing dense longitudinal columns of sarcosomes from between which a few fibrillar remnants (*f*) project. ( $\times 500$ .)

Fig. 5. A teased-out fragment of an atrophied muscle fibre (*A*) is contrasted with normal fibrillae and sarcosomes (*B*). ( $\times 600$ .)

Fig. 6. Portion of atrophied muscle fibre showing blackened spots in its substance which follow the distribution of the tracheoles

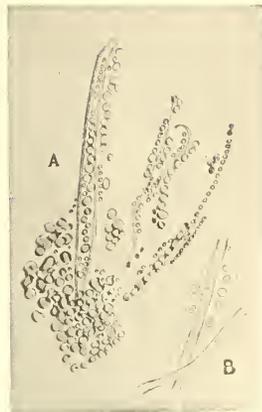
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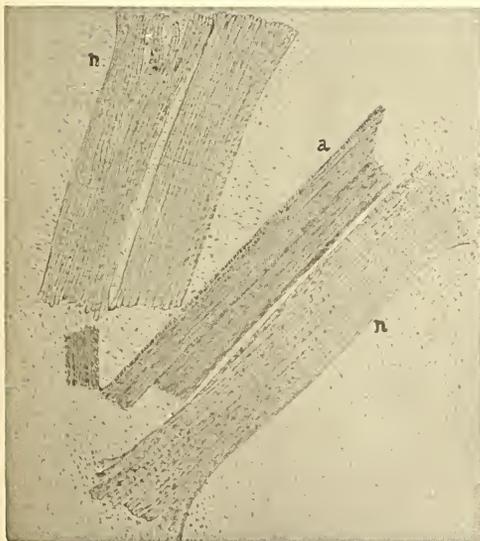
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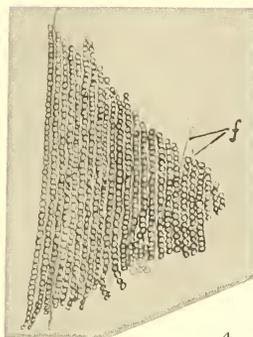
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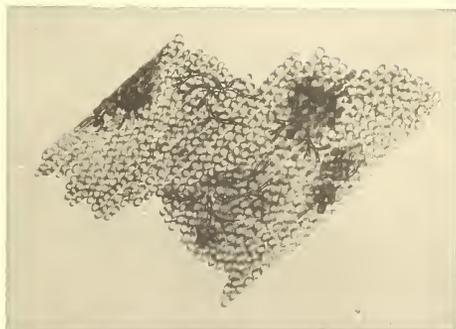
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## XXIX.

- (3) Isle of Wight Disease in Hive Bees—Experiments on Infection with *Tarsonemus woodi*, n. sp. By Elsie J. Harvey. *Communicated by* Dr JOHN RENNIE.

(Read November 1, 1920. MS. received November 27, 1920. Issued separately March 25, 1921.)

## INTRODUCTORY.

The following experiments and observations have been undertaken with a view to discovering the means by which *Tarsonemus* is transmitted from one bee to another. It is obvious that a stage of the parasite exists outside the bee, and that there are also several possibilities (which may occur). One is the passage from bee to bee within the hive either directly or through the medium of frames or combs. Another, also within the hive, where the mites may in wandering upon the frames enter the cells and invade the body of the developing larvæ or pupæ, and in this way be present in the bee when it hatches. A third possibility is that whereby foraging infected bees may leave the mite upon flowers, vegetation generally, drinking grounds, or other situations, to be picked up later by other bees chancing to visit these. Crawling or dead bees may in a similar manner prove to be a source of infection through the contamination of the ground about the hive or of the actual hive itself.

Exhaustive investigation of this last possibility is a somewhat difficult matter, for which no opportunity has yet been found, and owing to the short time at my disposal it has been set aside in favour of the more promising one of infection by direct contact between bee and bee.

## REVIEW OF FORMER EXPERIMENTS.

The conclusions arrived at from former experiments published before the organism was discovered, pointed to the probability of the disease being of an infectious character. This was shown when, *e.g.*, a frame of infected bees, say of a black colour, were placed in a healthy stock of Italians, and in due course the disease became evident in the yellow bees. It is admitted, of course, that only a probability is indicated in such an experiment.

What evidence we have from experiments with brood, in which frames of sealed brood of bees of one colour from an infected hive have been placed in the hive of a healthy stock of a different colour, points to the disease being an affection of adult bees only. Many experiments of this nature have been tried, and the results have been on the whole uniformly in favour of the view that brood hatched out under such circumstances was free from disease.

## EXPERIMENTS.

1. *To Discover whether Bees become infected before Emergence from Cells.*

Early in the spring of this year a few frames of brood from a badly affected stock were placed in an incubator; 155 of the bees which hatched out were examined, with the result that only the tube on one side in one bee was found infected with the parasite. This evidence, as far as it goes, therefore, does not exclude the possibility that mites may enter the cells and invade a bee's body before it emerges from the cells, but its rarity, as shown here, would seem to suggest that at best it is only an incidental occurrence, and is not one of the regular ways in which infection is conveyed.

2. *To Discover the Stage or Stages which occur normally outside the Bee.*

(a) By examination of the individuals in the tubes, in cases where the infection had only newly commenced, it is often found that an ovigerous female with a few eggs in different stages of development are the only parasites present. This would suggest that the migratory stage of the parasite is the fertilised female. In such a case migration of the male does not seem to be necessary, although, as is seen from the results of the experiments recorded, they leave the body of the dead bee.

(b) Equal numbers of living and of dead bees were placed in separate petri dishes, and these were kept as nearly as possible at the temperature of the hive. The dishes were examined microscopically at intervals of from two to forty-eight hours. Fifteen such experiments were carried out, with the result that only 10 mites, all of which were females, were recovered from the living bees: one of these was alive and active. As many as 75 (62 female and 13 male) were found in the dishes containing the dead bees. Of the 62 female mites, 8 were alive and active, while all the 13 males appeared dead. None of the females seen outside the bee were carrying fully developed ova. It would appear from these experiments that migration of both sexes takes place from the dead bee.

3. *An Endeavour to produce Infection artificially.*

(a) By contact with living sick bees.

These experiments were carried out in small queen cages. The bees were fed with soft candy and kept as far as possible at the temperature of the hive. The infective bees were in five cases crawlers picked up from in front of the hive; in two cases the bees were caught on entering the hive of a stock which was known to have a high per cent. of infection, and in the remaining three, the bees were taken from the frames of a sick stock. Virgin queens headed six of the experiments.

In these experiments the healthy bees were maintained in contact with sick bees for periods extending from four to seventeen days. In only one case was a positive

result obtained. On the fourteenth day of the experiment one bee was found to contain one ovigerous female at the entrance of the tube.

(b) By contact with dead bees.

Before commencing these experiments, observations were made to discover how long the parasites lived after the death of the host. It was found that a few female mites were still capable of feeble movement on the fifth and sixth days.

Seven of these experiments were put up in the same way as the foregoing, substituting newly killed bees for the living sick bees. The result in this group was negative.

(c) By placing tracheal tubes containing the parasite on the thorax of healthy bees.

Preliminary observations were made on the behaviour of the mites when the tubes had been dissected out of the bee. These were placed in wetted slides, and both sexes of the mites were seen to emerge within an hour. These wandered about actively, and were occasionally seen to re-enter the tubes. In most cases the mites became inert and passive within twenty-four hours of leaving the tubes. It cannot be said with certainty that in any of these experiments the mites are really dead.

Bees were now taken from a stock known to be free from infection, and tubes containing the parasite were placed on the thorax near the first spiracle. Twenty-four bees were treated in this manner, and were examined after twenty-four hours. It was found that no infection had taken place.

Examination of the stocks from which the experimental bees were taken, for the presence or absence of the parasite, were being regularly carried out.

It is to be clearly understood that the whole of the foregoing experiments are provisional in character, and all of them, as well as others, are being repeated upon a larger scale.

From the results obtained, as far as they go, however, it appears that experimental infection with the parasite *Tarsonemus* is difficult to effect; it must be taken into consideration that any deviation from the normal habits of the bee host such as is involved in these experiments may have a corresponding effect upon those of the parasite.

I wish to express my sincere thanks to Dr RENNIE, both for his help and advice in the preparation of this paper, and for his kindness personally whilst I have worked under him.

## XXIX.

- (4) Isle of Wight Disease in Hive Bees—Acarine Disease: The Organism associated with the Disease — *Tarsonemus woodi*, n. sp. By John Rennie, D.Sc. (With One Plate and Two Figures in the Text.)

(Read November 1, 1920. MS. received November 27, 1920. Issued separately March 25, 1921.)

The organism which has been found living in the anterior tracheal system of hive bees, and whose presence is associated with Isle of Wight disease, I have identified as a hitherto undescribed species of the genus *Tarsonemus*. This genus was founded in 1876 by CANESTRINI and FANZAGO, and since then a moderate number only of species has been established. The true systematic position of these Acarines has been much in doubt, and their position in the order has from time to time been revised. CANESTRINI (1888) constituted the Tarsonemes the type of a special family, the Tarsonemini; they have been associated with the Oribatidæ by BERLESE, and with the Cheyletidæ by TROUESSART (1892). BANKS (1904) regarded them as showing resemblances to the Tyroglyphidæ, and placed them in a super-family Sarcoptoidea. An important character of the Tarsonemes is the existence of a tracheal system in the adult female, which is not found in the male nor in any pre-adult stage of either sex. This feature was adopted by BERLESE (1897) as the basis of his sub-order, Heterostigmata, and by OUDEMANS (1906) in his division Trachelostigmata. This super-family includes two families—Tarsonemidæ and Scutacaridæ\* (OUDEMANS, 1916). This last is the Disparipedidæ of BERLESE.

The Tarsonemidæ are a small family of soft-bodied mites, the females of which are tracheate, and which usually exhibit prominent hairs upon the tarsi of the last pair of legs. The body is more or less clearly segmented dorsally. The mandibles are needle-like, the palps slender and minute. The females possess in most instances, between the first and second pair of legs, a pair of delicate rounded or club-shaped organs which have been designated pseudostigmata by OUDEMANS. The legs are short, with six or fewer joints. They are bedecked with a limited number of stout hairs, and terminate in claws. The tarsi of the first pair possesses a single claw, the second and third, two. The fourth tarsus varies in the different genera. Suckers are frequent. There may be distinct sex dimorphism, especially in the genus *Tarsonemus*.

## THE GENUS TARSONEMUS.

CANESTRINI'S original description defining the genus is as follows:—

“Rostro normale e libero. Zampe del quarto pajo nella femmina poco sviluppate, sformate di uncini e di ventosa e terminate da duo setole; zampe del primo pajo,

\* I desire here to gratefully acknowledge the courtesy of Dr OUDEMANS in guiding me to the literature of the Tarsonemidæ and Acarina generally.

pure nelle femmine, normali, conformate come quelle del secondo e terzo pajo, colla differenza che hanno un' unghia sola. Zampe del quarto pajo nel maschio robuste, costituenti insieme unachela, terminate da un' unghia robusta. Epimeri del terzo e quarto pajo nel maschio assai lunghi e forti e convergenti insieme verso l'avanti. Scudo dorsale diviso in segmenti. Animali viventi su piante."

The adult female of the species to be described conforms well to the generic characters given above, and cannot, in my opinion, be separated from the genus *Tarsonemus*. The only morphological character upon which such a separation could be based is the conformation of the fourth pair of legs, and possibly the absence of pseudostigmata (not included in the original generic description). The male is undoubtedly more specialised in the fourth leg characters, but to constitute a new genus upon this fact, or upon the parasitic habit with which this specialised feature appears associated, seems to me inadmissible, at any rate in the present state of our knowledge.

A distinctive feature of the genus *Tarsonemus* is the fourth pair of legs, which in the female are slender, terminate in two hairs, and are devoid of claws. In the male, in the gall-inhabiting and free-living species, the last pair of legs is robust and terminates in a claw-like segment, usually incurved and frequently strongly developed. In some of the species recorded as endoparasitic, these characters in the male appear less well marked, and in the main show a reduction in size of this pair of appendages. In the species to be described the hind legs in both sexes present, especially in the male, features which I regard as related to the parasitic mode of life and restricted habitat of the insect's tracheal system.

*Tarsonemus woodi*, n. sp.

I propose to designate this species, which is parasitic in the anterior thoracic tracheal system of the hive bee, *Apis mellifica*, and which does not appear to have been described before, by the name of *Tarsonemus woodi*, n. sp. The adult ovigerous female measures from '14 to '19 mm. in length, the male about '11 to '15 mm. (fig. 1). Viewed with reflected light, these mites are more or less bean-shaped in form, greyish in colour, and scantily bedecked with hairs. When removed from the tracheæ of the bee they progress slowly upon glass, but when seen within the tube, although continued observation has not revealed much progression, a good deal of active and vigorous leg movement may be observed.

OVIGEROUS FEMALE.—Seen from above, the body presents a somewhat oval form, broadest in the neighbourhood of the second pair of legs. The following are typical dimensions for a fully grown adult :—

Total length from tip of gnathosoma to hinder end of body, '19 mm.

Total length from tip of gnathosoma to tip of longest hair of fourth pair of legs, '25 mm.

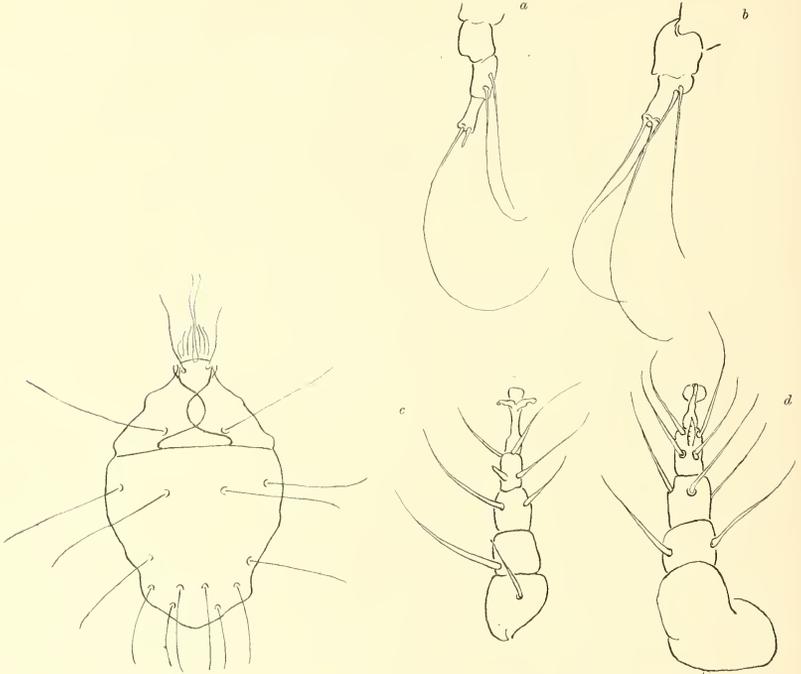
Width at broadest part of body, '10 mm.

Length of gnathosoma, '03 mm.

Length of first, second, or third legs, '05 mm.

Dorsally the body shows definite segmentation.

On the ventral side there is a distinct transverse furrow behind the second pair of legs. The gnathosoma is bluntly triangular and freely movable, and in



TEXT-FIG. 1.—Dorsal view of body of immature female, showing distribution of hairs. The anterior portion of the two main tracheae are shown.

TEXT-FIG. 2.  
a, Fourth leg of male; b, fourth leg of female; c, second leg of male; d, first leg of male.

the middle line in front the mandibles are frequently to be seen protruded as a pair of slender curved needles. The two anterior pairs of legs are directed forward or outwards, and some distance apart from the third and fourth pairs.

*Body Hairs.*—On the dorsal surface there are eight pairs of hairs fairly evenly distributed along the body (text-fig. 1). There is a short pair anteriorly, directed forward close to and upon each side of the gnathosoma, arising on the medial side of the stigmata. A second pair arises opposite the second pair of legs,

about one-third of the body width from the margin, and slightly in front of the dorsal furrow. Behind these are two pairs at about the middle of the body, one pair near the margin and the other in a nearly direct line behind the second pair. A pair arises nearly opposite the origin of the third pair of legs; behind these are two pairs constituting an almost straight transverse row, closely followed by a final pair close to the hinder end of the body, and separated by about a third of the width.

*Tracheal System.*—A pair of stigmata opening dorsally occurs anteriorly close to the base of the gnathosoma. From these the more dorsal and anterior portions of the tracheal system pass backward as a pair of curving, slender tubes, which cross each other at the level of the anterior limbs. These pass ventralwards curving inwards toward each other, and again outwards towards the bases of the posterior limbs.

*Legs* (text-fig. 2).—The anterior pair is jointed, and terminates in a single hook, with circular sucker in addition. On the penultimate segment upon the dorsal side there is a sensory spine-like organ—"riech-haar" of OUDEMANS. The second pair also carries a similar spine and ends in a double claw and sucker. The third pair of legs resembles the second, but a "riech-haar" is absent. These limbs arise near the margin and are directed outward and backward, and usually lie clear of the body for the greater part of their length. The fourth pair of legs, which arises closely behind the third pair, exhibits distinctive features. In contrast to what is usual in other species, instead of being long and slender, this limb is moderately stout at its basal segment and slender beyond. But the whole limb consists of only two segments and is much reduced in length. Upon it are four hairs, two of which are terminal and of considerable length. One of the remaining two arises nearer the base, but is usually seen along with the terminal hairs, forming a group of three projecting beyond the body (text-fig. 2, *b*).

IMMATURE FEMALE.—This differs in size and general shape, being more truncated behind (fig. 9).

Length of body from '13 to '15 mm.  
Width    "       "       '08 to '09 mm.

ADULT MALE.—The adult male is smaller than the female and more truncated in form behind.

Total body length '11 to '15 mm.  
                  "       width '06 to '08 mm.

Dorsally, it appears to consist of three segments, besides the gnathosoma. Only five pairs of hairs are present, all placed slightly inward from the lateral margin, and nearly equidistant along the side. On the ventral side the following features are observable. The transverse furrow behind the second pair of legs is well marked. There are no longitudinal epimeral grooves such as are prominent in most free-living

species. The external genitalia consist of two rounded lobes, projecting posteriorly on each side of a tapering triangular penial sheath.

*Legs.*—Special features regarding the limbs are: On the penultimate segment of the second pair of legs there is a prominent sensory organ. The fourth pair of legs is relatively slender, and presents the most distinctive characteristic of the species in this sex. There are three joints, all of which are comparatively weak; the terminal one bears the very long, stout, and finely curved hair distinctive of the genus. Just within this, and almost at the tip of the last segment, is a small straight spine, which occupies the position of the incurved terminal claw, characteristic of free-living species. Close examination has suggested that this structure is of the same character as that on the second pair of legs of the males, and on the female limbs also, and that it is probably sensory in function (fig. 7).

*LARVA.*—The larva is large, being about .2 mm. in length by about .08 mm. in width at its broadest part. The mouth parts resemble those of the later stages. There are three pairs of short legs; the first terminates in a double claw (fig. 4).

*OVUM.*—The egg is large, being about .14 mm. long by .06 mm. broad, and slightly concave along one side (fig. 2).

All the Heterostigmata appear to be parasitic, some on plants, others upon insects, and doubtfully on warm-blooded vertebrates. The majority of the described species of *Tarsonemus* are found upon plants; the others are from the bodies of vertebrate animals, in which a number have been found associated with malignant growths. *T. woodi*, n. sp., appears to be the only species known to occur in insects. Its discovery as an endoparasite within the hive bee therefore constitutes a significant advance in our knowledge of these mites, and of the general importance of the genus, apart from the far-reaching suggestiveness of its causal relationship to a disease in hive bees which has baffled inquiry for the last sixteen years.

As giving a more detailed indication of the habits of the genus, the following brief references to the best-known species are submitted. In view of the importance of habit and habitat in the case of *T. woodi*, I have preferred to refer to these, not in the order of their original discovery or description, but to group them from this point of view.

#### GALL-FORMING SPECIES.

*T. floricolus* Cn. and F., 1876.—This species is described as occurring on the flowers of *Verbascum*, forming galls in foliage of *Vitis vinifera*, *Coryllus avellana*, *Salix alba*, etc., in putrefying stuff, and in frass of bacon beetle. *T. (Cheylurus) socialis*, according to BERLESE, is of the same species. It is described from the skin and base of the feathers of birds of very diverse species, both terrestrial and aquatic.

*T. buxi* Canestr. and B., 1884.—Occurs as an inquiline in *Phytoptus* galls and in *Diplois* galls. See CANESTRINI (1886), pp. 320-1.

*T. canestrini* Massal., 1897.—Forms small rounded galls on several European grasses.

*T. phragmitidis* Schlechtendal, 1897.—A species resembling *T. canestrini*, which occurs as an inquiline in phragmitid galls.

*T. contubernalis* Reuter, 1906.—An inquiline in galls upon *Galium verum*.

*T. latus* Banks, 1904.—Causes galls on the main shoots of the mango plant.

*T. intectus* Karpelles, 1885.—In barley; producing severe irritation on hands of workers in the Danube region in Hungary and Russia.

*T. spirifex* Marchal, 1902.—On grasses; causes elongated swellings on oat. Occurs in colonies.

DESCRIBED AS DOING DAMAGE TO PLANTS BUT NOT APPARENTLY ASSOCIATED  
WITH GALLS.

*T. oryzae* Targ., 1878.—Infests the ears of the rice plant.

*T. culmicolus* Reuter, 1900.—From spikes of meadow grass; produces "silver top" in grasses in Finland, where it is found in the leaf sheaf above the uppermost node.

*T. anasæ* Tryon.—Described as causing injury to pine apples in Australia.

*T. fragaria* Zimmerm., 1904.—Has been found on strawberries.

*T. graminis* Kramer, 1886.—So named by Kramer because it occurs in abnormally rolled-up grass leaves.

*T. bancrofti* Michael.—Has been described as causing damage to sugar-cane in Queensland and in Barbados.

DESCRIBED FROM ANIMALS.

*T. floricolus*.—Already quoted above as occurring in the bases of birds' feathers.

*T. soricola* Oudms., 1903.—Found on *Sorex vulgaris*.

Regarding the placing of these species here, it may be mentioned that OUDEMANS is of opinion that when forms occur on animals these are probably no more than transporting agents.

*T. hominis* Dahl, 1910.—From human ovary in carcinoma and fibroma, and from bladder in cystitis (BLANC and ROLLET, 1910).

*T. sauli* Dahl, 1910 (*T. equi*; *T. muris*; *T. canis*).—From tumours in mammals.

*T. woodi*, n. sp., Rennie, 1920.—In thoracic tracheæ of *Apis mellifica*.

In this connection reference should also be made to a form described by MYAKE and SCRIBA (1893) from the urine of the human subject as *Nephrophages sanguinarius*. According to OUDEMANS this form is a *Tarsonemus*. It is tracheate, blind, has needle-formed manibles, and the pear-shaped pseudostigmatic organ has been mistaken for eyes. According to him the mouth parts are not described or figured correctly.

The group of species which have been obtained from mammalian tissues presents

some features of interest in relation to *T. woodi*, and it seems worth while considering these in some detail. DAHL has described a species termed by him *T. hominis*, which was obtained by E. SAUL, the female from a fibroma of the human ovary, and the male from a carcinoma of the same organ. Later in the same year, SAUL published micro-photographs of *T. hominis* and of others obtained from a cancer of the mouse, a papilloma of a horse, and a sarcoma of a dog. Following the publication of SAUL's photographs, BLANC and ROLLET (1910) published a statement that they had in their possession an acarid obtained in 1909 from the urine of a patient suffering from a refractory cystitis. They describe the specimen in detail and recognise it as a male of *T. hominis*.

*T. hominis* is distinguished, according to DAHL, from all previously described species by the following. In the female the fourth pair of legs is more shortened than in other species. Except for the end bristles it does not reach to the hinder end of the body. The third pair has a longer, thinner, two-segmented end part sharply marked off from the basal segment by the greater width of the latter. The two bristles at the hind end of the body are wider apart than is the case in other species. The male is distinguished from all other known males by the size and thickness of the long bristle at the end of the last pair of legs, and by the presence of a thick, club-shaped appendage on the second pair of legs (riech-haar of OUDEMANS). Both sexes are further differentiated by the course of the epimeral grooves on the posterior ventral surface.

DAHL groups all the forms from mouse, horse, and dog tumours as *T. sauli*. Amongst these there are two males, distinguished from *T. hominis* in that, of the five longitudinal furrows, the three innermost are united by a well-developed transverse furrow, and the sensory organ on the second pair of legs is not more developed than in the first pair. In the females constant distinguishing characters could not be made out. He states that the same difficulty applies to the females from gall-inhabiting species.

Mr STANLEY HIRST has kindly directed my attention to the fact that the conclusions of DAHL have been severely criticised by REUTER (1910) both as regards the probable accidental introduction of the mites in question to the preserved tissues from which the preparations were made, and as to the identity of the species. It appears to me that DAHL has not shown sufficient care in differentiating the forms found from species already described.

#### AFFINITIES OF *TARSONEMUS WOODI*, n. sp.

DAHL (1910) regards the genus *Tarsonemus* as representing a transitional stage between the gall-forming mites, Eriophyidæ or Phytoptidæ, and other mite families. He bases his conclusions largely upon the characters of the fourth pair of legs. In the species which are not endoparasitic in animals, but lead a life in relatively free space and where mating may be effected in the open, the fourth pair of legs in the

male is relatively large and of robust build, and terminates in a stout curved spine. These features are regarded as of value in mating. In the male of *T. hominis* this limb appears definitely smaller in size and general build in proportion to the other parts as compared with other species. DAHL interprets this as related to an endoparasitic life. In view, however, of our very slight knowledge of this species, and especially on account of the doubt which exists as to its normal habitat, the conclusion must be received with reserve.

If we apply such a comparison to *T. muris* and *T. equi* (*T. sauli* Dahl), these occupy an intermediate position between such a species, e.g., as *T. floricolus* and *T. hominis*, and so far affords some support to DAHL's view.

Including *T. woodi* in this comparison, we regard its place as undoubtedly at the end of the series. *T. woodi* agrees with *T. hominis* in general appearance in both sexes, but in detail more closely in the male than in the female. In the male they agree in possessing on the second pair of legs a sensory organ (riech-haar of OUDEMANS) of relatively large size as compared to the one on the first pair. The reduction in size of the last pair of legs is also a common feature, although in *T. woodi* the whole limb is markedly slighter in build than in *T. hominis*. With respect to the terminal claw also the comparison is interesting. In *T. hominis*, though showing the inward curvature characteristic of the genus, this is smaller than is the case in all the hitherto known species. In *T. woodi* the limb appears to terminate in a straight, sharp spine. The mite has been seen carrying this spine directed inwards at right angles to the limb. Under a high power it exhibits an appearance similar to that of the sensory organ upon the anterior limbs, and there is doubt as to its homology with the terminal claw present in other species. Whatever view we take regarding the reality of the endoparasitism in *T. hominis*, etc., I incline strongly to the view that these special features in *T. woodi* are to be interpreted in relation to the fact that the habitat of the male is probably limited to the tracheæ of the host, and also that mating takes place in this confined space. These conditions largely obviate the necessity for specialised clasping limbs. At the same time a sensory organ on the limb would obviously be of value.

Another feature worthy of notice is found in the nature of the ventral surface, which is devoid of the five longitudinal epimeral grooves which are prominent in most species, including some of those which are regarded as endoparasitic in mammalia, e.g. *T. hominis*.

In the female of *T. woodi* fewer points of comparison can be laid hold of. The most noteworthy are to be observed in the two hinder pairs of legs. These in *T. hominis* and in *T. sauli* are comparatively weak and slender. In both cases the fourth pair terminates in the usual two long bristles. In *T. woodi* the fourth pair is not slender, but is reduced to three segments, is somewhat stumpy, and its two bristles are long and sweeping. Pseudostigmata have not been described in any of the so-called endoparasitic species, and they have not been observed in *T. woodi*.

Reviewing the main features of *T. woodi*, it appears that there are good grounds for regarding this as a species of specialised structure in relation to the particular habitat in which it lives.

#### BIOLOGICAL CONSIDERATIONS.

I now propose briefly to consider the biological problem presented by *T. woodi* in relation to Isle of Wight disease.

For the final acceptance of the thesis that *T. woodi* is exclusively responsible for the condition known as Isle of Wight disease, careful consideration must be paid to the biological aspect of the problem.

I. Although the numbers of bees examined from outside Great Britain in relation to those from within have been comparatively few, yet considerable numbers have been tested. Through the assistance of the Ministry of Agriculture, bees arriving in this country accompanying queens from Italy have been obtained in a number of cases for examination.

In all, several hundreds of bees were obtained from this source. These, along with others obtained direct from Italy, were searched for the presence of *Tarsonemus*. The result of these examinations was that the bees were found entirely free from the parasite. The evidence is so far satisfactory that it may be accepted that *Tarsonemus* is not being introduced to this country in Italian bees. Smaller numbers of Dutch bees so imported have also yielded on examination a similar result. Bees in limited numbers have also been obtained from Switzerland and from North America, all of which were also free from this parasite. The evidence is not complete by any means, but, as far as it goes, it is of one kind. Since this disease has never been clearly demonstrated to exist outside the British Isles, nor certainly any epizootic approaching in any way the dimensions of Isle of Wight disease in the British Isles, and further, since all such evidence as we possess points to a causal relation between *Tarsonemus* and Isle of Wight disease in bees, this coincidence in distribution is noteworthy. If a geographical distribution limited to Britain should be established in the hive bee—and to do this is a mere matter of time and favourable opportunity—in my opinion it would point to a relatively recent invasion of the bee, although the opposite finding would not be against such a view.

It may be noted that ZANDER (1911), who has paid particular attention to the recording of pests found in hives and upon hive bees in Germany, makes no reference to Acarids of any kind. In the course of our investigations we have found in hives or upon combs, dead or live bees, at least five different species, including one other species of *Tarsonemus*.\* These mites will be dealt with in a subsequent publication.

\* In *C. R. Acad. Paris*, t. 62, 1866, M. EMIL DUCHEMIN records the occurrence of a microscopic *Acarus* on diseased hive bees. He gives no description nor figure. This is clearly not an endoparasite, since M. DUCHEMIN found that it bred upon sunflowers protected from the bees.

II. Morphology, development, and habits all point to the fact that this is a parasitic organism which must have been related to the tracheal system of some host for an indefinite period. The habit is not new. If *T. woodi* has been a parasite of bees for ages, it seems improbable that the disease phenomena which accompany its presence, and such as we are now familiar with, could have escaped notice. On the other hand, it may be that, although the parasitic relationship is not new, the pathology is. But such is not very probable.

It is true that, as far as bee records go, there have been in the past periods of epizootic disease in bees from time to time, but there is no evidence that a continuous epizootic extending from sixteen to eighteen years has taken place.

III. It may be suggested that earlier methods of bee-keeping, whereby destruction of bees was annually resorted to, kept down this parasite. This would certainly have been the case, if the parasite were present, and the method should be applied to all existing diseased stocks before winter. But surely the disease would then, as now, have manifested itself constantly in the working season to a degree sufficient to attract attention. And it must be remembered that modern methods of bee-keeping are not confined to Great Britain and Ireland.

IV. May it not be that *Tarsonemus*, owing to some unknown change in the normal balance of inter-relations, is at present undergoing one of those periods of undue increase such as occurs from time to time in various animal forms. We must recognise that it may be a parasite of bees which normally does not attain such an incidence as to attract special notice, and that in recent times there has been some change in the "balance of nature" which has led to its excessive increase. Bee-keeping has increased in Britain within the last twenty-five years; can it be said that, apart from the ravages of this disease, our Islands are overstocked? This again is unlikely.

V. It has been suggested that British bees of the present time are of a deteriorated breed, and have lost resisting power, so that *Tarsonemus*, a relatively non-pathogenic parasite ordinarily, is able to breed excessively. My provisional answer is that other racial forms are similarly affected. For example, Egyptian, Dutch, Punic, and Italian bees can be readily infected, and in these *Tarsonemus* multiplies with disastrous results, as in British bees. But the question of the ability of a stock to survive a prolonged period of *Tarsonemus* infection is not a simple one; amongst other factors, it involves the question of relative fertility of particular queens, as well as that of individual tolerance of the parasite (p. 753).

VI. *Tarsonemus* may be relatively new to hive bees and normal to some other insect.

There remains the possibility that *Tarsonemus* exists normally in some wild insect—possibly a hymenopteron—related to the hive bee, and that invasion of the bee is recently established. In such a case, the unknown normal host will remain a potential reservoir of the parasite.

It is noteworthy that many species occur on plants, but, as has been shown, these, as far as known, do not possess the specialised characters of *T. woodi*, and for this reason it seems improbable that bees have recently become infected from flower-haunting forms. It is more probable that this took place through contact with other insects, possibly robbing visitors to hives.

It may be remarked that along with my colleagues I have examined numbers of wasps, humble bees, earwigs, wax moths, *Braula caeca*, and although other mites were readily found upon the exterior, particularly upon the earwigs, the thoracic tracheæ in all cases were found clear.

The importance of finding answers to all of these questions raised is fully recognised by the Investigation I have the honour to direct, and the work is continuing with unabated vigour. I desire to take this opportunity of thanking my colleagues for the skill and ability with which they have aided me in the work so far accomplished, and particularly Miss ELSIE HARVEY, my personal assistant, whose loyalty and diligence have been noteworthy.

The foregoing researches have been carried out under the Joint-Committee upon Animal Nutrition of the University of Aberdeen and the North of Scotland College of Agriculture, with the aid of grants from the Development Commission, together with the generous financial help of A. H. E. WOOD, Esq., of Glassel. To all of these, for their valuable assistance, and to the Local Advisory Committee, under Professor JOHN ARTHUR THOMSON, whose encouraging advice has been unflinching throughout, I desire to express the cordial thanks of my colleagues and myself. I also desire to thank the Carnegie Trust for help in connection with this research.

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## EXPLANATION OF FIGURES.

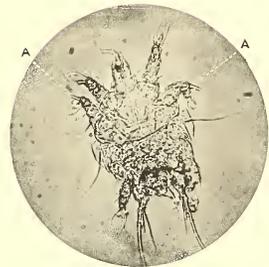
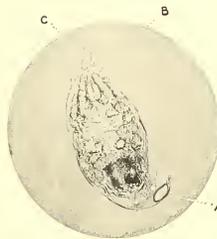
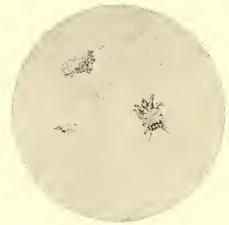
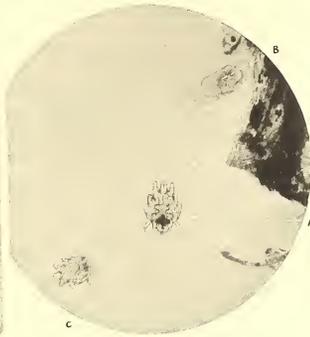
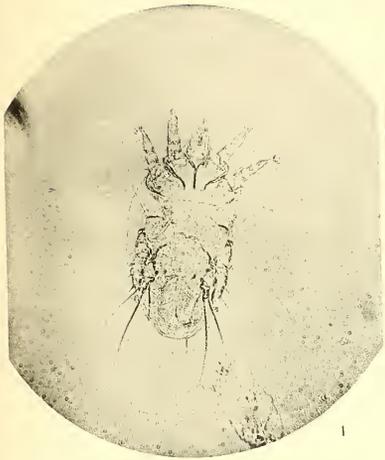
*Tarsonemus woodi*, n. sp. Microphotographs.

(All the preparations are photographed with a Watson Service Microscope.)

Fig. 1. Adult female, ventral view. Obj.  $\frac{1}{6}$  in. Ocular No. 4.Fig. 2. A, young tracheate female; focussed on ventral side to show tracheae. B, ovum. C, a male.  
Obj.  $\frac{2}{3}$  in. Ocular No. 4.Fig. 3. Adult male. Obj.  $\frac{2}{3}$  in. Ocular No. 4.Fig. 4. Larva. Focussed to show double claw on first pair of legs. Obj.  $\frac{1}{6}$  in. Ocular No. 4.Fig. 5. Larva containing nymph. Focussed to show the latter: a female. Out of focus: A, posterior end of larva. B, first pair of legs of larva. C, gnathosoma of larva. Obj.  $\frac{1}{6}$  in. Ocular No. 4.Fig. 6. Male. Focussed to show sensory organ, A, on second pair of legs. Shows also spine on fourth pair of legs. Obj.  $\frac{1}{6}$  in. Ocular No. 2.Fig. 7. Posterior end of male, showing last pair of legs and external genitalia. A, spine. B, genital lobes.  
Obj.  $\frac{1}{6}$  in. Ocular No. 4.Fig. 8. Teased trachea showing: A, adult female. B, immature female (tracheate). C, two males.  
Obj.  $\frac{2}{3}$  in. Ocular No. 4.Fig. 9. Female, showing tracheae. Obj.  $\frac{1}{12}$  in. Ocular No. 4.



RENNIE: ORGANISM ASSOCIATED WITH ISLE OF WIGHT DISEASE





XXX.—Shackleton Antarctic Expedition, 1914–1917: Depths and Deposits of the Weddell Sea. By J. M. Wordie, M.A., F.G.S. *Communicated by* Professor J. W. GREGORY, F.R.S.

(MS. received December 6, 1920. Read February 7, 1921. Issued separately May 27, 1921.)

#### INTRODUCTORY.

Previous to the voyage of the *Endurance* in 1914–1915, the depth and extent of the Weddell Sea were either based on or surmised from the deep-sea soundings made on the *Scotia* by Dr BRUCE in 1903 and 1904; on Dr OTTO NORDENSKJÖLD'S ship *Antarctic* in 1901–1902; and on the German Expedition ship *Deutschland* under the leadership of Lieut. FILCHNER in 1912–1913. The first set are confined to the eastern and north-eastern portion, and may be said to run diagonally across the mouth of the sea; the second set were made in the extreme north-western area; whilst those of the *Deutschland* are disposed right down the centre of the sea, and consist mainly of a south-to-north series approximately along the meridian of 43° W.

In the early part of her voyage the *Endurance* was on ground partly covered by the *Scotia*, and she was thus able to supplement very considerably Dr BRUCE'S work off Coats Land; in January and February 1915 her track crossed that of the *Deutschland* at about a right angle; thereafter it lay on entirely new ground to the west of all previous routes. She drifted right across that unknown tract which some map-makers have called New South Greenland, and the majority of people Morrell Land.\* Apart, therefore, from the importance which attaches to the soundings by reason of their being on ground previously unexplored, they are also of value inasmuch as they definitely prove that "Morrell's land" is no part of the Antarctic continent, and probably does not exist even as an island.

#### EQUIPMENT.

The instruments used for sounding were three in number: a Lucas machine graduated up to 5000 fathoms; a smaller machine of the same type for depths of 1000 fathoms; and a Kelvin machine registering up to 300 fathoms. By splicing on additional wire, however, it later on became possible to use the Kelvin for depths of 450 fathoms. This, of course, meant that the dial, which was arranged for a 300-fathom drum, did not register quite accurately for 450 fathoms of wire. It must have slightly under-registered, but there was no opportunity of actually checking the error; in any case, it can hardly have been as much as 1 per cent., and can well be neglected.

\* MORRELL himself called it "New South Greenland," and stated that it had been discovered by Captain JOHNSON. To refer to it as "Morrell's land," rather than "Morrell Land," would be more correct.

The type of attachment employed for collecting bottom samples varied with the machine. In the case of the Lucas, there was used either a snapper or a group of four short tubes, each about 4 inches in length and  $\frac{1}{2}$ -inch diameter; both were fitted with a detachable weight of 50 lbs. In the smaller Lucas machine, the 28-lb. weight was not detachable; this machine, however, was very seldom required, and was finally stowed away as unnecessary. In the case of the Kelvin a 14-lb. sounding lead was at first in use, but later on a snapper with fixed weight (belonging to the small Lucas machine) was found to give better samples. When the deposits ultimately became so monotonous that they were no longer desirable as specimens, a return was made to using the simple 14-lb. lead. Experience showed that in Antarctic waters the snapper is the best all-round form of attachment.

This equipment was found to be quite adequate to its purpose.\* Sufficient detachable weights were carried to take one hundred deep-sea soundings. As the great majority of the casts, however, were made in shallow waters where a machine with recoverable sinker could be employed, not quite half of these weights had been used up to the time when the ship was crushed and had to be abandoned. It is hardly necessary here to give details or hints on the methods.† It may be mentioned, however, that winding-in was done by hand; in the case of the deeper soundings (1500–2000 fathoms) this took almost an hour.

#### POSITION OF THE SOUNDINGS.

While the ship was a free agent and fighting her way southwards through the ice, soundings were made whenever she was held up by close pack. The ship's course was never interrupted to take a sounding, for the number of times both in the pack and off Coats Land when she was stationary was quite sufficient for the purpose. After she was beset (January 1915), casts were made more frequently, and, when the depths became moderate, sounding became a routine task practically every forenoon. Later (August 1915), when deep water was again met with, an attempt was made to sound twice in every degree of latitude. This at least was what was aimed at; the programme only lasted for a short time, however, as at the end of October the ship was crushed and abandoned, and sounding gear was naturally not among the essentials salvaged from the wreck.

In the Table of Soundings the positions up to and including January 19, 1915 (when the drift commenced), are those at which the sounding was made, calculated by dead reckoning from an observed noon position. Onwards from January 20, however, the positions entered are the daily noon positions observed by the ship's officers; their

\* This was the only branch of oceanography which was well provided for—a result, of course, of planning the scientific equipment of the Expedition almost entirely for a base on land. In view of the opportunities for oceanographical work, whether the ship is beset or not, it is desirable that this science, as it was on the *Scotia* voyage, should be well in the forefront of the programme of any future expedition.

† Dr PRIE gives very full and useful information about methods, etc., in his report.

accuracy, by reason of the occultation observations obtained during the winter, is of the order of one nautical mile.\* During the latter period the ship was drifting in the ice at an average rate of four sea miles per day. As the soundings were practically all made within three hours of noon, none of them are likely to be distant from the latter position by more than one mile—that is to say, they differ by no more than the possible error of the ship's noon position.

#### DEPOSITS.

The actual samples were all abandoned when the ship was crushed. At the time they were collected, however, brief notes were always made, and these are quite sufficient to provide a short geological description.

Everywhere in the Weddell Sea the deposit was found to be terrigenous in origin; in keeping with PHILIPPI and PIRIE, the term "Glacial Mud (and Clay)" is therefore employed. PIRIE rather emphasises the distinction between glacial mud and glacial clay; on board the *Endurance* it was not thought necessary to do so, or indeed practicable without a detailed examination of the deposit. In the table the term "Glacial Mud" covers both muds and clays. Where the deposit was sandy, or where pebbles were commoner than usual, attention is drawn to these features. The origin, of course, of a deposit such as this glacial mud—namely, the agency of drifting ice—makes the presence of rocks from the size of a pebble up to boulders weighing several hundredweights everywhere possible. Traces of sand should also have the same wide distribution; yet a deposit which could be truthfully called sand rather than mud was something unusual.

In former days this characteristic deposit of Antarctic waters was classed as "Blue Mud." Everything terrigenous in origin found below 100 fathoms (if not separated off into the small subdivisions such as Volcanic and Coral Muds) was in fact liable to be put down as such. This cannot have been Sir JOHN MURRAY's original intention, but after the publication of the *Challenger* volume the term certainly had a tendency to become almost synonymous with a deep-sea terrigenous deposit. For these Antarctic muds, however, the term was by no means a fortunate one. To begin with, the deposit in question characterises the continental shelf as well as oceanic depths. The colour, moreover (owing probably to deficiency in organic matter), is practically never blue, but rather dark grey or brown to brownish-grey. As a rule, when dried it becomes lighter in colour. Blue Mud, for these and other reasons detailed by PHILIPPI, can no longer be considered a fit name. A subdivision of the same standing as Volcanic or Coral Mud is necessary. PHILIPPI and PIRIE have accordingly adopted Glacial Mud as being the most suitable term. To sum up: Glacial Mud differs from most terrigenous deposits in being found not only in shallow water (*i.e.* on the shelf which in the Antarctic is 200, not 100, fathoms

\* The occultation observations have since been checked by Mr A. C. D. CROMMELIN of Greenwich Observatory, and the positions adjusted accordingly by Mr JAMES, physicist to the Expedition.

in depth), but also in depths of as much as 2000 fathoms; it differs from Deep-Sea Terrigenous Deposits in there being no arrangement of the constituents according to size, the transporting agency being a solid, namely, ice; and it differs from Blue Mud both in colour and in the fact that there is practically no carbonate of lime present in the deposit and very few organic constituents.\*

As regards the Weddell Sea deposits, PIRIE seems to imply that the distribution of clay lies farther out from the continent than the mud. On the *Endurance*, however, it was noticed that deposits on the shelf were fully as worthy of being called clays as those from deep water, at least as far as macroscopic evidence went. The consistency, indeed, of the bottom deposit might vary very rapidly in a very small area. One day the lead would plunge in to the depth of a foot into soft mud, and the next, but a few miles away, sink only about half an inch into tough clay.

Sand or grit was frequently present, but never in large quantity except off Coats Land, where some of the deposits were labelled as sand rather than mud; and in 70° S. lat., 40° W. long., where for the space of a week in the middle of April 1915 the deposits were all very sandy. This unusual feature makes it quite possible that at the latter place the *Endurance* was nearer land than at any other time after leaving Coats Land; absolutely no sign, however, of what might be land was seen from the crow's-nest.

The proportion of rock fragments, mainly small pebbles, was highest along the Coats Land coast. Pebbles and boulders, however, were likely to occur at any time, and particularly when a bottom sample was procured by means of the dredge. These rocks were always very carefully examined (as hand specimens, and not under the microscope) in view of the complete lack of knowledge of Coats Land geology. Considering the ice-bound nature of that land, it seems very unlikely that exposures of rock will ever be found there in any quantity, so that any data, however scanty, obtainable from bottom samples such as these must be of value.

#### GEOLOGY OF THE ROCK-FRAGMENTS.

The rock specimens obtained directly off Coats Land are best treated separately from those got farther west in the Weddell Sea, as their source is not so much a matter of doubt. On January 12, 1915, in 74° 07' S., 23° 02' W., a dredging was made in 103 fathoms and brought up a sandy deposit full of sponge fragments and small pieces of rock. Among the latter, granite with white felspar was the commonest igneous rock; basalt and dolerite were not quite so abundant; a grey grit was much the commonest sedimentary rock, and a purple sandstone was found, but not in any quantity. At a later date, in 76° 34' S., 31° 27' W., the dredge yielded, in addition to granite with white felspar, another variety with hornblende and red felspar;

\* MURRAY and RENARD's classification as given in *The Depths of the Ocean*, p. 161, requires a slight alteration accordingly. "Glacial Mud (and Clay)" should be inserted after "Coral Mud," grouped on the one side with "Deep-Sea Deposits" and on the other with "Terrigenous Deposits."

basalt also occurred, and a rock which was provisionally classed as a peridotite. On other occasions grit (both red and green), shale, and pebbles of hard mud were obtained. The shales were generally marked with glacial striæ. On all these occasions the glacial mud which formed the bulk of the sample was extremely sandy. Among the material collected, two rock types only could be called common, namely, grey granite and grits, grey to green in colour. Some of the sediments recalled the Beacon Sandstone of Victoria Land in general appearance, but they were never sufficiently distinctive types to warrant one in saying definitely that Coats Land geologically resembles the lands east of the Ross Sea.

The remainder of the dredgings were made farther out from land; but there is every reason for saying that here, as well as nearer Coats Land, the source of the material was to the east. This conclusion is founded on the clockwise motion of the Weddell Sea ice, proved by the *Deutschland* and *Endurance* drifts. Among these later dredgings shale, quartzite, and green grit were the commonest rocks; grit particularly was very common. On March 26, 1915, in  $76^{\circ} 27' S.$ ,  $38^{\circ} 43' W.$ , the haul was remarkable for including a red grit boulder weighing over 70 lbs., and a block of limestone (with fossils) about half that weight. Another block of similar limestone was brought up not ten miles away a few days later. The specimens have, of course, been lost, but it is quite possible that two of them represent the *Archæocyathus* Lst. of Cambrian age, previously known from Victoria Land and from a *Scotia* dredging in  $62^{\circ} 10' S.$ ,  $41^{\circ} 20' W.$  Other sediments identified were oolitic limestone, white and dark-grey quartzite, arkose (noted as being fairly common), banded shale, spotted shale, and chert. Of igneous rocks there was a considerable variety. Granite, although a hornblende variety with red felspar is noted more than once, was never so abundant as farther east. Dolerite, however, was common. Peridotite appears again, also pitchstone, porphyrite, and quartz felsite; diorite and basalt sometimes occurred, but not often. On one occasion a fragment possibly of tuff was obtained, but its identification was apparently a matter of doubt. Metamorphic rocks were represented by gneiss, garnetiferous gneiss, and mica-schist. None of the igneous or metamorphic rocks, however, occurred in quantity at all comparable to grey grit and white quartzite.

On the whole the data are insufficient for determining whether Coats Land is geologically similar to Victoria Land or to Graham Land. The balance of probability has always been in favour of the former alternative. The *Endurance* observations, however, do not bring the problem any nearer solution, but they have certainly produced nothing to render it improbable that Coats Land, like Victoria Land, belongs to the plateau type of Antarctica.

#### BATHYMETRICAL RESULTS.

Previous bathymetrical maps of this area have in two instances put down hypothetical contours over the region explored by the *Endurance*. BRUCE on the

one hand has crowded his contours in a somewhat unnatural way to ensure "Morrell's land" being part of the Antarctic continent. BRENECKE of the *Deutschland*, on the other hand, in prolonging his 1000-, 2000-, and 3000-metre depth-contours has made them sweep across to Graham Land in natural curves, and to the south-west of them has inserted the term "Flachsee." The result of the *Endurance* soundings definitely removes "Morrell's land" from the realm of probability, and substantiates practically all that BRENECKE had inferred as likely to occur in the west. His "Flachsee" has proved to be a remarkably shrewd guess, though it still remains doubtful what grounds he had for inferring such a broad continental shelf.

The main results of the *Endurance* soundings are these:—

(1) The 1000-, 1500-, and 2000-fathom lines apparently sweep across without disturbance from Coats Land to Graham Land, passing south and west of the position where MORRELL claimed land and where ROSS charted "strong appearance of land" (but without, however, deeming it sufficiently important or well founded to mention it in his book of travels).\* The latter "land" was first called in question when NORDENSKJÖLD made a sounding of 2050 fathoms within thirty miles of ROSS's "appearance of land." The behaviour of these contours, therefore, makes "ROSS's land" and "Morrell's land" highly improbable. It is true that there is plenty of room for an island here; but it would have to rise from oceanic depths, and the rule for other Antarctic islands is that they are generally linked to the continent by a rise or something similar. Such cannot be the case here. Moreover, there are very good grounds for concluding that MORRELL's chronometer was far from correct, making (if his "north-east cape of New South Greenland" is Joinville Island) his positions fully eight degrees too far east; if his statements are to be believed, the land off whose coast he claims to have been sealing was simply the east coast of Graham Land. Map-makers of the future, therefore, are hardly likely to insert land in 68° S., 48° W., unless it is vouched for by someone else besides this somewhat discredited American sealer.

(2) The 500-fathom line follows a much more irregular course, and at one point is deflected south as far as the face of the Wilhelm Barrier. This suggests the existence just here of a deep channel, with a somewhat sinuous course, running south approximately between the 36th and 37th meridians.

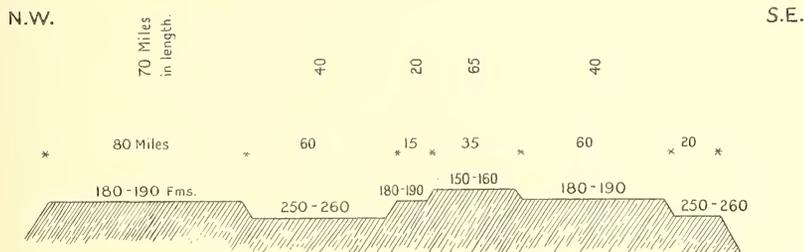
(3) East of the above-mentioned deep channel the bottom shoals gently towards Leopold and Caird Coasts. The continental shelf off Coats Land is in fact comparatively narrow. Deep water, therefore, is found off such features as the protruding Stancomb Wills Promontory, a barrier remnant of a once larger area; under the ice-cliffs 676 fathoms, no bottom, and ten miles off a depth of 1355 fathoms were recorded. The shelf is narrow but by no means regular; the soundings of the three expeditions which have visited Coats Land make it pretty certain that although that

\* ROSS in his narrative (vol. i, pp. 177-178) tells how his inexperienced officers were often deceived by appearance of land, and would not be persuaded that it was otherwise until they had actually sailed over the place.

country is now completely ice-covered, except for some nunataks in the extreme south in 78° S. lat., the solid rock below is nevertheless sculptured into hills and valleys. This is indicated not only by the irregularity of the soundings, but also by the uneven, mountainous character of the snow-covered land itself.

(4) West of the deep channel down the centre of the sea there is a somewhat sharper rise than to the east; and there are also more uniform conditions on the shelf itself. The *Endurance* drifted on to the shelf in the last week of March 1915. Up till then the total number of casts which had found bottom was thirty-five; besides these, there were some doubtful and some incomplete soundings, not without importance. Once on the shelf, soundings could be made without the sinking weight having to be sacrificed each time; a daily cast therefore became the rule. From March 31 till July 31 (both inclusive) 103 soundings were made. All of these were in depths under 275 fathoms.

In a way this series of soundings on the continental shelf was unique, and it would have been a matter of surprise if some important result had not been the outcome of it all. The majority of the soundings clustered round 180-190 or 250-260 fathoms. Over a large area the depth was about the same, day after day, and then it would suddenly change to another level. The back and forward drift of the ship now had its uses, for the numerous soundings are so distributed as to



The stepped terraces on the continental shelf. Vertical scale much exaggerated. The most north-westerly terrace is eighty miles broad, and at least seventy in length (*i.e.* from south-west to north-east), and so on.

prove the existence of a series of stepped terraces with boundaries running N.E.-S.W.; these run at right angles, apparently, to the presumed coast line farther to the south-west, but are parallel to the known coast line of the Leopold and Caird Coasts of Coats Land. The stepped terraces extend from 76° 18' S., 38° 23' W., to 72° 37' S., 47° 47' W., a distance of about 270 sea miles. The line so measured (*i.e.* across the terraces) represents very nearly the mean course of the ship's drift from S.E. to N.W.; at the same time, however, she was drifting sometimes more to the north-east, at other times more to the south-west; and in neither direction did the water show the least sign of shoaling. The extent of this shallow area therefore came to be known as at least forty miles across in the south-east, and over seventy

in the north-west. These terraces are shown diagrammatically on the accompanying figure. The slope from one terrace to another is of course much distorted; if drawn to scale it would be almost imperceptible, as it works out on the average at only 1 in 200.

On the east coast of Graham Land the Charcot Expeditions have shown the shelf there to be at least one hundred miles broad and of similar depth to what it is in the Weddell Sea. In the past indeed the Antarctic continental shelf has aroused considerable interest by reason of its depth being double the average depth of the shelf round the other continents—200–250 as against 100 fathoms. PHILIPPI, commenting on this, thought it might be due to planing down by ice during the once greater extent of the Antarctic ice-cap. NORDENSKJÖLD, on the other hand, thinks there may be some connection between the existence of the great Antarctic ice-cap and a resulting land submergence. The terraced structure, which the *Endurance* observations show, at once disproves PHILIPPI'S idea. These features, however, can be explained by faulting;\* and it may therefore be the case that the deep Antarctic shelf here and elsewhere is the result of earth movement of some sort rather than of erosion.

(5) The slope of the continental edge as deduced from the *Endurance* figures is 1 in 62. This result is certainly misleading; for unfortunately the edge was crossed in a three-day blizzard at the beginning of August 1915, when the ship was in considerable danger and sounding therefore of secondary importance. There is an interval of forty miles or more in which to place the edge; the 185-fathom sounding is just over sixty sea-miles from a depth of 1146 fathoms. The sounding of 370 fathoms, no bottom, is of practically no value, as it is only ten miles from 1146 fathoms. That the edge is much steeper than 1 in 62 is more than likely, judged by the paired soundings of other expeditions. The steepest slope recorded by any Antarctic expedition is 1 in 17, and the average 1 in 26; the real slopes, moreover, will probably be a trifle steeper, as the chance that a ship crossed the edge at right angles is small. The *Endurance* figure should therefore be put aside.

	Sounding on Shelf.	Sounding in Deep Water.	Distance Apart in Sea-miles.	Slope.
<i>Belgica</i> . . . . .	279	1476	25	1 in 29
<i>Gauss</i> . . . . .	209	1267	18	1 ,, 17
<i>Scotia</i> . . . . .	159	1950	45	1 ,, 25
<i>Deutschland</i> . . . . .	305	820	18	1 ,, 35
<i>Endurance</i> . . . . .	185	1146	60	1 ,, 62

(6) In the forefront of all bathymetrical work in the American sector of Antarctica is the question of the one-time relationship to each other of the various island groups which border the Weddell Sea to the north. On this important point, however, the

\* NORDENSKJÖLD states that Bransfield Strait is due to faulting.

*Endurance* results have nothing fresh to bring forward. Much that is new has, indeed, been found in recent years and been published, mainly in foreign periodicals. Such are, for instance, the finding by the Swedish Expedition of a rise between Joinville Island and the Powell Group, and the extremely important line of soundings made by the *Deutschland* between the South Orkneys and the South Sandwich Group. The latter show not a simple rise, but a series of alternate rises and deeps trending E.—W. and perhaps linking these two island groups. Reference may also be made to a rock reported by a whaler in 1916 as lying in latitude 58° 31' S., longitude 41° 48' W. Much more evidence, however, is certainly required before it can be decided whether the necessary link between the geologically similar regions of Graham Land and Patagonia connects all the island groups forming the so-called Southern Antilles, or passes somewhat more to the west, as Professor GREGORY would have it.

*Table of Soundings.*

Abbreviations :—K = Kelvin machine; L = Lucas; S. L. = Small Lucas; l = lead; sn = snapper; t = tubes; Gl.m. = Glacial mud or clay.

No.	Date.	Position.		Depth in Fathoms.	Depth in Metres.	Machine.	Attachment.	Nature of Bottom.	Remarks.
		Latitude S.	Longitude W.						
	1914								
1	Dec. 18	62 42	18 14	(2810)	(5139)	L.	...	Very doubtful sounding.	
2	" 26	65 43	17 36	2819	5155	L.	sn.	Gl.m., brownish-grey in colour. The consistency is like that of clay. Under the microscope fragments of quartz and of some coloured mineral were noticed.	
	1915								
3	Jan. 6	70 44	21 25	2400	4389	L.	...	Gl.m., brownish-grey. Quartz fragments very common; besides other unidentified minerals.	
4	" 10	72 02	16 07	200	366	K.	...		
5	" 10	72 43	18 47	210	384	K	...	Barrier edge only about 100 yards distant.	
6	" 11	73 20	20 55	155	283	S. L.	sn.	Pebbles and sand grains; the former include dolerite and basalt (? with olivine). At this point barrier cliff turns sharply to S.E.	
7	" 11	73 29	21 50	190	347	S. L.	l.	Stony bottom. (A sounding half an hour later gave 210 fathoms, no bottom.)	
8	" 12	74 06	22 51	95	174	(S. L.	sn. )	Pebbles (of grit), sand, and mud.	
9	" 12	74 10	22 58	128	234	(K.	l. )	Greenish-brown sand, pebbles, and mud; sponge spicules, and foraminifera.	
10	" 12	74 07	23 02	103	188	K.	sn.	Sand and pebbles. A dredging made in this position brought up a mass of sponges. The bottom deposit was sandy, with many pebbles (the largest 2 inches across) of:—Grey grit, common; purple sandstone; granite with white felspar, common; basalt; dolerite; syenite (possibly).	
11	" 13	74 2	26 12	675	1236	...	...	Stancomb Wills Promontory bore E. 2½ miles.	
12	" 14	74 10	27 21	1355	2478	L.	sn.	Gl.m., greyish-brown. No pebbles.	
13	" 15	75 2	25 25	268	490	L.	sn.	Gl.m., somewhat sandy, with a few pebbles.	
14	" 15	75 20	26 41	120	219	K.	l.	Some sand on the arming.	
15	" 16	76 26	28 40	134	245	K.	l.	Sand grains and sponge spicules.	
16	" 16	76 22	28 31	136	249	K.	sn.	Pebble of hornblende-granite, coated with bryozoa.	
17	" 19	76 34	31 27	312	570	L.	sn.	Gl.m., bluish-grey, sand, and small pebbles. A dredging made later in the day brought up sandy mud with pebbles of:—Peridotite (possibly); granite with white felspar; granite with red felspar; arkose; basalt; pebbles of indurated mud.	

Table of Soundings—continued.

No.	Date.	Position.		Depth in Fathoms.	Depth in Metres.	Machine.	Attach- ment.	Nature of Bottom.	Remarks.
		Lati- tude S.	Longi- tude W.						
18	Jan. 20	76° 39'	32° 08'	270	494	...	...	Very doubtful sounding.	
19	" 21	76 44	32 45	350	640	L.	sn.	Gl.m. and sand; about half a dozen small pebbles.	
20	" 22	76 49	33 22	337	616	L.	sn.	Mud, dark grey, sand, and pebbles.	
21	" 25	76 48	33 36	382	699	L.	sn.	A fish trap which was in use came up filled with waterlogged mud, sand, and a few pebbles, the latter include shale and hornblende-granite with red felspar.	
22	" 26	76 50	33 57	360	658	K.	sn.	The fish trap was in use at a depth of about 355 fathoms. It filled with sand, mud, and pebbles:—Hornblende-syenite; red grit; green grit; shale (some pieces showing glacial striae).	
23	" 28	76 46	34 05	449	821	L.	sn.	Gl.m., dark grey; very little sand and a few very small pebbles.	
24	" 29	76 47	34 12	449	821	L.	sn.	Gl.m., dark grey; very little sand and a few pebbles.	
25	Feb. 1	76 49	34 31	510	938	L.	sn.	Gl.m., dark grey, a trifle sandy; a few small pebbles.	
26	" 3	76 50	34 47	520	951	L.	sn.	Gl.m., dark grey, sandy.	
27	" 4	76 53	34 38	520	951	L.	sn.	Gl.m., dark grey.	
28	" 6	76 53	34 48	530	969	L.	sn.	Gl.m., dark grey and sandy.	
29	" 8	76 55	35 01	529	967	L.	sn.	Gl.m., dark grey, sand, and small rock fragments; dark grey mud when dried becomes light dusty grey in colour.	
30	" 13	76 50	35 18	529	967	L.	sn.	Gl.m., dark grey.	
31	" 19	76 55	34 54	522	955	L.	sn.	Gl.m., dark grey.	
32	Mar. 5	76 53	35 54	561	1026	L.	sn.	Gl.m.	
33	" 18	76 53	37 17	606	1108	L.	sn.	Gl.m.	
34	" 22	76 37	38 15	442	808	L.	sn.	Gl.m.	
35	" 23	76 37	38 22	443	810	L.	sn.	Gl.m.	
36	" 24	76 36	38 22	419	766	L.	sn.	Dredge brought up much Gl.m., together with pebbles of black shale and grit.	
37	" 25	76 32	38 37	406	742	L.	t.	Gl.m.	
38	" 26	76 27	38 43	380	695	L.	t.	Gl.m., light grey, at least 2 inches deep.	
39	" 27	76 22	38 50	358	655	L.	t.	Dredge was down twice. The first haul yielded a porphyrite pebble 3 inches across; the second brought up numerous pebbles of grit and shale besides a block of red grit 70 lbs. in weight, and one of fossiliferous limestone 7 inches across.	
40	" 30	76 20	38 28	338	618	L.	...	Gl.m. A Rutherford tube was used for the first and only time.	
41	" 31	76 18	38 23	256	468	K.	l.	Dredge brought up a block of fossiliferous limestone 6 inches across.	
42	Apr. 2	76 17	38 24	262	479	K.	l.	Gl.m.	
43	" 3	76 17	38 34	264	483	K.	l.	Dredge besides abundant mud contained two small pebbles, one a mica schist.	
44	" 4	76 9	38 30	250	457	K.	l.	Gl.m.	
45	" 5	76 9	38 43	245	448	K.	l.	Dredge included a few small pebbles.	
46	" 6	76 12	39 04	244	446	K.	l.	Gl.m.	
47	" 7	76 18	39 48	242	443	K.	l.	Gl.m., slightly gritty.	
48	" 9	76 29	40 14	273	499	K.	l.	Gl.m., gritty.	
								Dredge brought up sandy mud. Two pebbles, one a limestone, the other an oolite.	

Table of Soundings—continued.

No.	Date.	Position.		Depth in Fathoms.	Depth in Metres.	Machine.	Attachment.	Nature of Bottom.	Remarks.
		Latitude S.	Longitude W.						
49	Apr. 10	76° 27'	40° 09'	253	463	K.	l.	Gl.m., gritty.	Dredge contained a block of white grit about the size of one's hand.
50	" 11	76 24	40 03	255	466	K.	l.	Gl.m., gritty.	Dredge contained pebbles of:—Grey shale; quartzite; grit; diorite (?).
51	" 12	76 14	39 14	238	435	K.	l.		
52	" 12	...	...	232	424	K.	l.		Sounding made about six hours later than No 51.
53	" 13	76 04	39 20	212	388	K.	l.	Gl.m. and sand.	
54	" 14	75 59	39 13	197	360	K.	l.		
55	" 15	75 54	39 16	192	351	K.	sn.	Gl. sand and mud.	
56	" 16	75 55	39 31	192	351	K.	sn.	Sand and pebbles.	
57	" 17	75 57	39 41	196	358	K.	sn.	Moist sand and mud.	
58	" 18	75 57	39 49	193	353	K.	sn.	Gl. m.	
59	" 19	75 59	40 11	181	331	K.	sn.	Firm dark grey sand and mud.	
60	" 19	...	...	177	324	K.	l.		Sounding about six hours later than No. 59.
61	" 20	76 00	40 48	178	325	K.	sn.		
62	" 20	...	...	178	325	K.	sn.		Sounding about six hours later than No. 61.
63	" 21	76 03	41 48	181	331	K.	sn.	Sand, mud, and pebble.	
64	" 22	76 01	42 01	180	329	K.	sn.	Gl.m. and sand.	
									Dredge yielded over 100 pebbles up to 3 inches across. For the most part they were rounded and enclosed in tough sandy gl.m. Some appeared to be faceted:—Grey grits, common; quartzite, white; pink grit; arkose, fairly common; dolerite, common; diorite; granite with pink felspar; granite-gneiss; garnetiferous gneiss; peridotite (possibly); chert breccia; spotted shale; shales.
65	" 23	76 02	41 48	179	327	K.	sn.	Gl.m.	
66	" 25	75 56	41 40	178	325	K.	sn.	Gl.m.	
67	" 26	75 49	41 42	179	327	K.	sn.	Gl.m.	
68	" 27	75 45	41 42	177	324	K.	sn.	Gl.m., stiff.	
69	" 28	75 38	41 33	174	318	K.	sn.	Gl.m.	
70	" 29	75 29	41 25	169	309	K.	l.	Gl.m.	
71	" 30	75 25	41 43	172	314	K.	l.	Gl.m.	
72	May 1	75 27	42 00	175	320	K.	l.	Gl.m.	
73	" 3	75 22	42 18	175	320	K.	l.	Gl.m.	
74	" 4	75 23	42 26	173	316	K.	l.	Gl.m.	Fish trap was lowered and filled with bluish-grey gl.m.
75	" 5	75 19	42 26	170	311	K.	sn.	Gl.m. and sand.	
76	" 6	75 10	42 20	161	294	K.	l.	Gl.m. with a little grit.	
77	" 7	75 07	41 52	159	291	K.	l.	Gl.m. and a little grit.	
									Dredge filled with 2 feet of tenacious mud. About a dozen pebbles:—Arkose; grits, white and pink; green igneous rock.
78	" 8	75 03	42 17	162	296	K.	l.	Gl.m., slightly gritty.	
79	" 10	74 59	42 06	152	278	K.	l.	Gl.m., light grey, gritty to the feel.	
80	" 11	75 00	41 58	157	287	K.	l.	Gl.m.	
81	" 12	75 08	41 54	157	287	K.	l.	Gl.m., gritty.	
82	" 13	75 19	42 22	170	311	K.	l.	Gl.m., very little grit.	
83	" 14	75 23	42 52	163	298	K.	l.	Gl.m.	
84	" 15	75 27	43 09	161	294	K.	l.	Gl.m.	
85	" 16	75 26	43 37	153	280	K.	l.	Gl.m., very slightly gritty.	
86	" 17	75 24	43 57	157	287	K.	l.	Gl.m., slightly gritty.	
87	" 18	75 23	44 01	156	285	K.	sn.	Gl.m., slightly sandy.	
88	" 20	75 27	44 26	155	283	K.	l.	Gl.m., with a little sand.	
89	" 21	75 24	44 45	155	283	K.	l.	Gl.m., with a little grit.	
90	" 22	75 23	44 59	157	287	K.	l.	Gl.m., light grey; practically no sand.	
91	" 24	75 22	45 45	165	302	K.	l.	Gl.m., light grey.	
92	" 26	75 14	44 54	172	314	K.	l.	Gl.m.	Dredge contained following pebbles:—Quartzite, white; chert; grits; dolerite (?); shale, black and grey.
93	" 27	75 04	44 51	187	342	K.	l.	Gl.m.	

Table of Soundings—continued.

No.	Date.	Position.		Depth in Fathoms.	Depth in Metres.	Machine.	Attach- ment.	Nature of Bottom.	Remarks.
		Lat- itude S.	Longi- tude W.						
94	May 28	74° 59'	44° 56'	197	360	K.	1.	Gl.m., dark grey.	
95	" 28	...	...	205	375	K.	1.	Gl.m., grey (brownish); no sand. Sounding about twelve hours later than No. 94.	
96	" 29	74 55	44 41	204	373	K.	1.	Gl.m. Dredge brought up a few pebbles:—Quartzite, dark grey; slate.	
97	" 30	74 46	44 57	224	410	K.	1.	Gl.m.	
98	" 31	74 49	45 30	253	463	K.	1.	Gl.m., grey.	
99	June 2	74 47	45 12	254	464	K.	1.	Gl.m.	
100	" 3	74 45	45 05	256	468	K.	1.	Gl.m., slightly gritty.	
101	" 4	74 44	44 57	256	468	K.	1.	Gl.m.; colour had a bluish tinge.	
102	" 5	74 43	44 55	254	464	K.	1.	Gl.m., grey.	
103	" 7	74 32	45 03	256	468	K.	1.	Gl.m., grey; no grit.	
104	" 8	74 27	45 13	258	472	K.	1.	Gl.m.	
105	" 9	74 26	45 23	259	474	K.	1.	Gl.m., slightly sandy.	
106	" 10	74 25	45 28	259	474	K.	1.	Gl.m.	
107	" 11	74 27	44 45	254	464	K.	1.	Gl.m. Minute ice crystals present in the mud; make determination of grittiness by feel quite impossible.	
108	" 13	74 29	46 21	259	474	K.	1.	Gl.m.	
109	" 14	74 30	46 21	258	472	K.	sn.	Gl.n., brownish-grey.	
110	" 15	74 33	46 23	258	472	K.	1.	Gl.m.	
111	" 17	74 39	46 39	252	461	K.	1.	Gl.m.	
112	" 18	74 37	46 48	255	466	K.	1.	Gl.m. Dredge brought up mud with very few pebbles. One of these is a white quartzite, 3 inches across.	
113	" 21	74 30	47 39	260	475	K.	1.	Gl.m.	
114	" 22	74 21	47 39	262	479	K.	1.	Gl.m.	
115	" 24	75 02	47 23	249	455	K.	1.	Gl.m.	
116	" 25	73 57	47 18	239	437	K.	1.	Gl.m., grey. Dredge contained numerous subangular and angular pebbles;—Hornblende-granite with red felspar; arkose; quartz felsite; quartzite; grits, grey and green, common; pitchstone; indurated mud pebbles.	
117	" 26	73 58	47 17	238	435	K.	1.	Gl.m.	
118	" 28	73 59	47 20	255	466	K.	1.	Gl.m., grey.	
119	" 29	74 03	47 29	260	475	K.	1.	Gl.m.	
120	July 1	74 08	47 54	255	466	K.	1.	Gl.m. Dredge brought up mud; no pebbles.	
121	" 3	74 11	48 39	226	413	K.	1.	Gl.m.	
122	" 4	74 09	48 50	203	371	K.	1.	Gl.m.	
123	" 4	...	...	194	355	K.	1.	Gl.m., brownish. Sounding made twelve hours later than No. 122.	
124	" 5	74 06	49 08	184	336	K.	1.	Gl.m., brownish. Dredge yielded nearly 60 pebbles:—Grits, quartzites (white), very common; shales; tuff (?); gneiss; garnetiferous gneiss; diorite or gabbro; felsite; basalt; arkose.	
125	" 6	74 06	49 11	185	338	K.	1.	Gl.m., with very small rock pieces. Instead of plunging the usual distance of about 1 foot into the mud the lead only went in $\frac{1}{2}$ inch. Gl.m., distinctly sandy.	
126	" 7	74 07	49 14	192	351	K.	1.	Gl.m.	
127	" 8	74 08	48 59	192	351	K.	1.	Gl.m.	
128	" 9	74 06	49 20	192	351	K.	1.	Lead absolutely clean.	
129	" 11	74 06	49 17	189	346	K.	1.	Little mud in cup; otherwise lead clean.	
130	" 13	74 12	48 57	190	347	K.	1.	Mud only in cup.	
131	" 16	73 36	48 27	202	369	K.	1.	Gl.m., brownish-grey; lead nearly clean.	
132	" 17	73 38	48 28	196	358	K.	1.	Gl.m., covering lead to depth of 1 foot.	
133	" 20	73 26	48 05	190	347	K.	1.	Gl.m., 6 inches deep.	
134	" 21	73 26	48 07	190	347	K.	1.	Gl.m., brownish-grey. Dredge yielded:—Grits, quartzites, 40-50 pebbles $\frac{1}{2}$ -3 inches across; granite with red felspar.	
135	" 22	73 19	47 50	185	338	K.	1.	Gl.m.	
136	" 24	73 07	48 12	186	340	K.	1.	Gl.m.; lead sank very deep in mud.	
137	" 25	72 59	48 04	187	342	K.	1.	Gl.m., 8-10 inches.	

Table of Soundings—continued.

No.	Date.	Position.		Depth in Fathoms.	Depth in Metres.	Machine.	Attach-ment.	Nature of Bottom.	Remarks.
		Latitude S.	Longitude W.						
138	July 26	72° 51'	47° 34'	189	346	K.	l.	Gl.m., 6 inches.	
139	" 27	72 47	47 36	190	347	K.	l.	Gl.m., 6 inches.	
140	" 28	72 44	47 34	188	344	K.	l.	Gl.m., 6 inches.	
141	" 29	72 40	47 34	189	346	K.	l.	Gl.m., 10 inches.	
142	" 30	72 39	47 34	187	342	K.	l.	Gl.m., dried to light grey colour. Pebble of white quartzite.	
143	" 31	72 37	47 47	185	338	K.	l.	Gl.m.	
144	Aug. 4	...	...	370	677	K.	...	Sounding made three hours earlier than No. 145. Ship drifting rapidly.	
145	" 4	71 50	48 41	452	827	L.	l.	Doubtful sounding, owing to lightness of sinker.	
146	" 5	71 42	49 16	1146	2096	L.	t.	Gl.m., light grey, 6 inches deep.	
...	" 10	...	...	...	...	...	...	Extremely doubtful sounding on this date.	
147	" 12	71 03	49 40	1550	2835	L.	t.		
148	" 17	70 38	49 54	1676	3065	L.	t.	Gl.m., light grey.	
149	" 25	70 09	50 08	1900	3475	L.	t.	Gl.m., grey.	
150	Sept. 6	69 54	50 22	1850	3383	L.	...	Gl.m., light grey.	
151	" 20	69 38	50 35	1856	3394	L.	t.	Gl.m., light grey.	
152	" 28	69 32	51 12	1876	3431	L.	t.	Gl.m., grey.	

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XXXI.—Shackleton Antarctic Expedition, 1914–1917: The Natural History of Pack-Ice as observed in the Weddell Sea. By J. M. Wordie, M.A., F.G.S. Communicated by Professor J. W. GREGORY, F.R.S. (With Nine Text-Figures and Four Plates.)

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C O N T E N T S.

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I.—INTRODUCTION.

The opportunities for observation were afforded by the voyage and subsequent drift of the S.Y. *Endurance*. During December 1914 and January 1915 for a period of six weeks she successfully bored her way through pack-ice of every description—drift-ice, open-pack, and very frequently even close-pack. Continually fighting, she penetrated from 59° to 72° S. lat., and finally reached the land water off Coats Land on the latter parallel. As the crew flies, therefore, she was navigated through ice for nearly 800 geographical miles on this voyage; her actual course among the ice-fields and floes was computed to exceed 2000 miles, an achievement without parallel in the Antarctic. The principle adopted was to keep to the east, where presumably there is less pack than in the west; if the *Endurance* experience is a normal one, however, the meridian of 20° W. long., which was followed, is certainly not far enough east.

The exploration of Coats Land and the discovery of Caird Coast followed, until the ship was finally beset on January 19, 1915. From that date until October 1915 she drifted northwards and westwards round the Weddell Sea at an average rate of four sea-miles per day, till finally crushed and abandoned on October 27. Thereafter the crew tried to sledge to land; or, camped on the ice, drifted from the position where the ship was wrecked (69° S. lat.) through a further seven degrees of latitude. So passed a second summer in the ice; and it was not till April 1916 that boats could be launched and escape effected, through the fringe of the pack, to Elephant Island.

These seventeen months of close association in some form or other with pack-ice have led to an opportunity of studying its origin and decay, and some of the laws governing its behaviour, which has never before been afforded to a British expedition in the Antarctic. The conclusions thus obtained, particularly as regards the westerly drift, will, it is hoped, be of use to all future Antarctic navigators.

From comparative study it appears as if the sea-ice cycle round the North Pole is much the same as in the South—spread, however, over a longer period and

influenced by much higher summer temperatures. The Arctic ice, however, has never been subjected to quite the same methods of observation, and it is therefore better to regard this paper as the natural history, not of pack-ice in general, but of Weddell Sea pack-ice.\*

*Historical.*—Previous to 1820 the idea seems to have prevailed that no ice formed at sea. DAINES BARRINGTON and HIGGINS, for instance, tried to reconcile the reports (now known to be erroneous) of whalers, that all ice found at sea was fit to drink, with the fact that sea-water frozen in the laboratory was fairly salt; they maintained, accordingly, that “no considerable congelation ever takes place in the sea,” and that the floating ice observed in high latitudes is land-derived. In 1820, however, SCORESBY, with the experience of many whaling voyages behind him, published what appears to be the earliest scientific account of the Arctic pack-ice by the actual observer himself. He demonstrated for the first time that ice could form on the sea far from land, and also showed how this ice might sometimes be fresh enough for drinking purposes. The mistake made in the next four decades was to imagine that freshness was the rule—a misconception which persisted till WALKER, who accompanied M’CLINTOCK as surgeon on the *Fox*, published his results in 1860. References to ice in the Franklin Search Expeditions are of course numerous, but very seldom reliable; and practically none of the writers except RAE take account of the physical and chemical side of the subject. RAE in later life read a short paper on some of his observations to the Physical Society, and made GUTHRIE sufficiently interested to make further experiments.

When in the seventies interest became once more directed to the Arctic, a good deal more attention than formerly was paid to the natural history of sea-ice. Both PAYER and his associate WEYPRECHT published clear and direct accounts of what they saw. On the Nares Expedition, however, ideas on sea-ice became again somewhat confused; the term “palæocrystic,” for instance, was introduced to include “floebergs” and heavy floes. NARES himself thought floebergs were due to direct freezing of sea-water; but MOSS, and later GREELY, realised that they were due to accumulated snowfall; and many years later PEARY actually found them forming from glaciers on the north coast of Greenland. The “palæocrystic floes,” on the other hand, are now regarded as simply hummocky-pack and heavy floes; later travellers over the Polar Sea, however, have done little to advance knowledge in this respect.

In more recent years PETTERSSON, DRYGALSKI, and HAMBERG have made considerable additions on the physical side. PETTERSSON’S results especially call for mention, for, if accepted, they are of extreme importance; BUCHANAN and others, however, have taken exception to his work. It now remains for someone to test in nature what PETTERSSON found in the laboratory.

\* In the forthcoming *Ice Memoir of the Scott Antarctic Expedition, 1910-1913*, Mr PRIESTLEY proposes to give an account of the Ross Sea fast-ice and pack-ice.

Slowly, piece by piece, the Arctic pack has come to be known, but a great deal still requires to be done. A useful summary of present-day views is given in KRUMMEL'S *Handbuch der Ozeanographie*. The Antarctic pack, however, has never had the same attention paid to it. FRICKER made a short compilation in 1893; but more important, as it was the record of actual observation, was ARCTOWSKI'S memoir in the *Belgica* Results. SCOTT, FERRAR, GOURDON, PRIESTLEY, DAVID, MAWSON, and others have all in turn contributed additional knowledge. Not through them, but in spite of their accounts, an impression seems, however, to prevail that Antarctic pack is of very different nature from Arctic; to this the strongest exception must be taken. Wrong ideas on sea-ice have never been short-lived; it is to be hoped, therefore, that the case of Arctic and Antarctic pack will not be prejudged till more is known about them both.

*Terminology.*—No new terms are introduced, beyond those suggested for the various types of cracks originating in the ice. The old terminology, used by the Arctic whalers, had a natural and practical origin, and is therefore followed as closely as possible. As there has been a slight tendency, however, for some recent Antarctic voyagers to alter the original use of a word, a restatement of some of the terms has become necessary; and a short glossary is therefore conveniently inserted here.

The best of all previous glossaries is, of course, that of SCORESBY, who was whaler before becoming scientist. A much fuller, and at the same time the most recent, list of terms is that of MARKHAM and MILL in the *Antarctic Manual*, 1901; most of their definitions cannot be bettered, but in others some slight modification seems desirable, since, after all, it is the navigators and sailors themselves who must have the last say. Where possible, however, the actual phrases of SCORESBY or of MILL are used here.

*Slush or Sludge.*—The initial stages in the freezing of sea-water, when its consistency is gluey or soupy. The term is also occasionally used for brash-ice still further broken down.

*Pancake-ice.*—Small floes of new ice, approximately circular, and with raised rims.

*Young-ice.*—All unhummocked ice, no matter of what age or thickness, which has platy structure and fibrous appearance when broken. Ice of this nature was formerly known in the Arctic as "bay-ice," but the term, unfortunately, has also been largely used in the Antarctic for "fast-ice," and for exceptionally heavy hummocky floes. With two such opposite meanings, "bay-ice" is therefore no longer of use for descriptive purposes.

*Fast-ice.*—Sea-ice which remains fast in the position of growth throughout the winter, and sometimes even during the ensuing summer. It may therefore attain a thickness considerably above the average. Other names for this type of ice are "land-ice" (PAYER and MILL), "Schelfeis" (DRYGALSKI), "shore-ice" (NANSEN), "bay-ice" (SHACKLETON and DAVID), and "coast-ice." If it is thought necessary to

employ a special name for fast-ice when it breaks adrift, "land-floes" is the most suitable; but generally it can be simply spoken of as heavy floes.

*Floe*.—An area of ice, other than fast-ice, whose limits are within sight. The surface of a floe may be level or hummocked, and in size it may vary from "pancakes" on the one hand to "fields" on the other. "Light floes" are between 1 and 2 feet in thickness; floes thicker than this are termed "heavy." The latter, however, often owe their thickness to hummocking, and in the Antarctic at any rate are usually covered with fairly deep snow.

*Field*.—An area of ice of such extent that its limits cannot be seen from the masthead.

*Crack*.—Any fracture or rift in sea-ice.

*Lead or Lane*.—A navigable passage through pack-ice. Leads may form either by the widening of a crack or by a general loosening of the floes. (On the *Endurance* voyage it was customary to speak of the former as leads even when covered with young-ice.)

*Pool*.—Any enclosed water-area in the pack other than a lead or lane. Pools may be of any size: those called "polynia" by Admiral Wrangel were so large as to give rise to the belief in an open polar sea.

*Frost-smoke*.—The fog-like clouds which appear over newly formed leads and pools, owing to the contact of the colder air with the relatively warm sea-water.

*Water-sky*.—The dark streak on the sky due to the reflection of leads or pools on the open sea.

*Ice-blink*.—The white or yellowish-white glare on the sky produced by the reflection of large areas of sea-ice. The antithesis of water-sky.

*Hummocking*.—The processes of pressure formation whereby level young-ice becomes broken and built up into hummocky-pack. "Tenting," "rafting," and "raftering" are terms in use to describe different phases of the process.

*Hummocky-floes*.—Floes composed wholly or partly of recemented pressure-ice. They have also been described as "old pack," "screwed pack" (DAVID), "Scholleneis" (German writers), and sometimes simply "pack-ice." In contrast to young-ice, the structure is no longer invariably platy or fibrous, but is generally spotted and granular. There is less salt present, and the ice may appear almost translucent.

*The Pack*.—Term used in a wide sense to include any area of sea-ice, other than fast-ice, no matter what form it takes or how disposed. The French term is "banquise de dérive."

*Close-pack-ice*.—Pack composed of floes mostly in contact.\*

*Open-pack-ice*.—The floes for the most part do not touch.\*

*Drift-ice*.—Loose, very open pack, where water preponderates over ice.\* The

\* Drift-ice is so open that ships can go full speed through it, and hardly ever need to change direction. In open-pack, on the contrary, the speed is slow and changes of course continually necessary. In close-pack a sailing-ship's course is generally completely checked, while steamers can only progress by repeatedly charging the ice.

floes are usually smaller than in close- or open-pack, being, in fact, the result of the first stage in the breaking down of the ice.

*Brash.*—Small fragments and rounded nodules: the wreck of other kinds of ice.

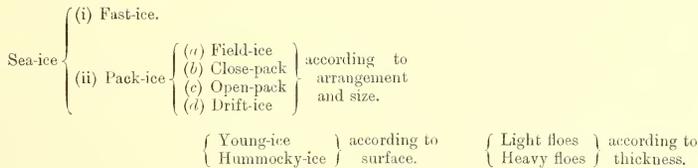
*Bergy-bits.*—Medium-sized pieces of glacier ice or of hummocky-pack washed clear of snow. (Typical bergy-bits have been described as being “about the size of a cottage.”)

*Growlers.*—Smaller pieces of ice than the above, appearing greenish in colour because barely showing above water-level.

*Rotten-ice.*—Floes which have become much honeycombed in the course of melting.

The above list is by no means exhaustive. There are many other terms of less importance, some of them being quite local, and many now obsolete. “Sea-bar,” “sailing-ice,” “tongue,” and “calf” seem to have gone out of use almost altogether. Drift-ice may collect into “streams” and “patches.” The pack edge may protrude as a “point,” or recede to form a “bight” or “bay,” etc., etc. Local terms are particularly numerous in Newfoundland, but are seldom found in print. Certain terms peculiar to navigation in pack-ice should also be mentioned: “sallying,” for instance, describes how a crew rolls a ship by dashing across from side to side in unison; a ship gets “nipped” or “beset” when open-pack closes up round her and stops all progress; and “boring” and “slewing” describe different ways of working through close-pack.

It will be gathered from the above definitions that sea-ice in the first instance is divided into (i) fast-ice and (ii) pack-ice. The latter is further subdivided, according to the arrangement and size of the floes, into (a) field-ice, (b) close-pack, (c) open-pack, and (d) drift-ice. The floes themselves in all four subdivisions may be of young-ice or of hummocky-ice, and light or heavy according to thickness. A chart of ice-conditions should first of all distinguish fast-ice and the above four subdivisions, and then, if necessary, specify the nature of the floes.\*



\* The Danish Meteorological Institute has for many years been publishing an annual chart of this nature for the ice in the Arctic. The naming, however, is slightly different from that adopted here. Six types of ice are distinguished, namely, “unbroken polar ice (i.e. fast-ice); land-floe; great ice-fields; tight pack; open ice; bay-ice and brash.” Certain of these names are no longer suitable in English. It will be noticed that four of the types depend on the *arrangement* of the floes, but two (land-floe and bay-ice), whose usefulness on the chart is open to doubt, on the *nature and thickness* of the floe itself.

## II.—EARLY STAGES.

*Formation.*—In the Weddell Sea, formation of new sea-ice took place both in rough water and in smooth; and the resulting structure differed accordingly. One had to distinguish, therefore, between young-ice formed in calm water, and ice formed on a ruffled sea. The former condition was found to be much the commoner; the latter was only noticed as a consequence of the very strongest blizzards, when the pack was completely broken up and rearranged. At no time during the voyage of the *Endurance* was the *open* sea seen to freeze over except in a dead calm; though in higher latitudes there should be no reason against a rough open sea freezing. The general rule, however, seemed to be for young-ice to form in the ever-opening pools and leads among older ice, as the latter offered protection by damping down any swell.

(1) *Growth of young-ice in still water* was studied very frequently in the leads, lanes, and pools which were continually forming at all times of the year. In 1915, when in lat.  $77^{\circ}$  S., young-ice was noticed for the first time on February 6, and a week later all leads began to freeze almost as soon as formed. This went on until October, when for new leads to freeze became unusual; the ship's position was then in lat.  $69^{\circ} 30'$  S. Water-skies were noted as being numerous on October 9; and on the 11th young-ice freshly formed on a pool had melted. In 1916, owing to the N.N.W. drift of the ice-floes on which various camps were situated, observations were made in much lower latitudes; young-ice did not start forming that year until the first week of March, and then only in a cold snap, the latitude at the time being  $64^{\circ}$  S.

The ideal opportunity for observing the first stages of ice-formation was such as was found on May 2, 1915. On that date a crack, formed in heavy hummocky pack, opened to a lead, and from a distance was seen to be giving off abundant frost-smoke. By reason of the crack having formed in heavy pack of composite origin, the bounding walls were seldom perpendicular; occasional tongues of ice jutted out into the water at various depths, and by reflecting up the light showed the intervening water filled with freely floating small platy crystals of ice about the size of a finger-nail. They had not yet arranged themselves or coalesced in any way, but seemed to fill the water for a depth of some feet. The water above such a jutting ice-tongue was probably chilled to a much greater depth than farther out in the lead, being bounded both below and on one side by ice, and above by the cold air; and this might account for the number of shimmering crystals in the water. As the crystals became more definite, they rose to the surface, and one could almost see them arranging themselves on to the film growing out from the edge of the lead. Such a fringe of young-ice was generally referred to as "black-ice"; the blackness, however, was largely due to contrast with the surrounding snow-covered floes. As a general rule it had a smooth but slightly damp upper surface formed of platy ice-

crystals (as already described) set horizontally. This is a feature first noted by FERRAR, and applies only to the uppermost  $\frac{1}{4}$ – $\frac{1}{2}$  inch; the vertical arrangement of the plates and grouping into bundles below the upper layer and throughout the rest of the ice have been noticed by all observers, and described and figured in detail, particularly by DRYGALSKI. This is the structure often referred to as platy or fibrous.

To the impression, however, given by FERRAR, that the upper layer is always formed of horizontally arranged plates, exception must be taken. A note of April 19 says "that from the edge of the old-ice thin narrow wedges (finger-like) extend out into the black-ice; these wedges have their apex against the old-ice and broaden as they go outwards, often reaching a length of 6 inches. They appear

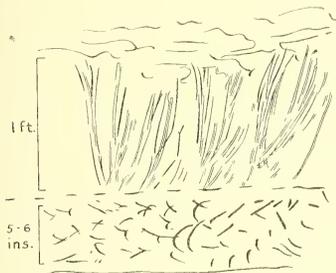


FIG. 1.

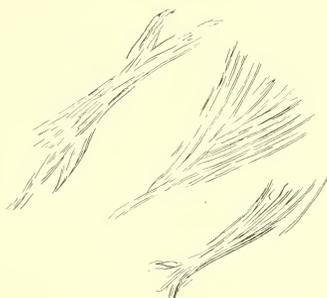


FIG. 2.

even darker than the surrounding black-ice, and the reason seems to be this: that they are made up almost entirely of plates set vertically." In the spaces between the wedges, however, the plates at the surface were set horizontally, reflected up the light a little, and did not appear so dark, therefore, as the wedges. Similar structures were frequently observed, and are apparently always to be expected where the water is bounded by a wall of old-ice at much lower temperature, from whose edge the young sheet can grow out. On May 2 a sketch was made of such a thin sheet in active process of growth (figs. 1 and 2).

Three bands, characterised by separate structures, were distinguishable. First of all, an irregular network 5 to 6 inches broad ran along the immediate edge of the old floe; then came a strip about 1 foot broad of radiating black wedges separated from each other by lighter interspaces; and still farther out was a third strip made up of an irregular mass of plates not yet systematically arranged on to the wedges. The second figure shows how irregular the wedges are, both in shape and in relative arrangement, and how the term "wedge" is simply one of convenience.

In the wedges the ice-plates are arranged vertically, or in an almost vertical position; in the interspaces horizontally arranged plates shade downwards into a

vertical series, and this latter position becomes the rule for further increase in thickness.

*Ice-flowers* were a common feature whenever newly formed cracks and leads froze over in winter; they were at their best when the temperature was below zero. They never remained perfect very long, however, for the clusters were generally rimed over in about twenty-four hours; or, since very low temperatures were rarely of long duration in 1915, a certain amount of remelting soon took place.

When ice-flowers were not present, young newly formed ice was always more or less soft and damp on the upper surface, owing to the temperature being generally higher than was conducive to their formation. On such a surface brine-bubbles were numerous, and were apparently potential nuclei for ice-flowers. Observations made on these bubbles in the end of May showed that, from originally being small and somewhat elliptical, they grew to be nearly an inch in length. In the "wedges" the axis of the bubble ran parallel with the length of the wedge; but in the interspaces, and where there was no guiding structure such as the wedge, the direction of the bubbles was quite fortuitous. Those which reached nearly an inch in length had been under observation for a week, when a fall of snow effectively prevented further investigation. Perhaps the earliest stage of the bubbles are the minute white specks such as were noticed on May 2 in black wedges of ice not twenty-four hours old. Elsewhere, and at different times, both the small rudimentary white specks and the undoubted brine-bubbles were often seen. It seemed pretty certain, indeed, that it only required a sudden drop in temperature for an ice-flower to form round such a bubble as nucleus.

The ice-flowers were only salt at the base, the distal crystal points being simply rime. Their irregular distribution, however, over a sheet of young-ice requires some explanation. A possible one is afforded by the way in which young-ice on a lead crystallises outward from the sides, and so takes different lengths of time to form, the resulting salt-content therefore being a variable one.

What has been described above either as "black-ice" a day or two old, or more generally as "young-ice," is simply what the Arctic whalers called "bay-ice." As ice formed in bays was always level, they also came to apply the term to undisturbed ice whether formed in bays or on the open sea. SCORESBY says: "Bay-ice is that which is newly formed on the sea and consists of two kinds, common bay-ice and pancake-ice; the former occurring in smooth extensive sheets, and the latter in small circular pieces with raised edges." "Bay-ice may be said to extend from the first pellicle of ice up to a foot in thickness." PAYER, BRUCE, and J. K. DAVIS use the term in its original and proper sense. In most of the Antarctic expeditions of the last twenty years, however, the name has unfortunately been used literally for ice formed in bays; in the Ross Sea, ice of this nature is sometimes almost a miniature tabular berg. The latter, so-called "bay-ice," will be referred

to here as fast-ice, or land-floes where adrift; and, to prevent confusion, "young-ice" will be always used to denote the old whalers' "bay-ice."

(2) Opportunities for seeing *young-ice forming on a rough sea* were of rare occurrence. One such, however, took place on July 15, when a blizzard opened a lead near the ship 300 yards in breadth. Crystallisation started almost immediately, and was materially helped on by the amount of blizzard-driven snow which had already formed a slush on the water surface. "It was like a rough frozen sea, for the slush had been rippled as it froze. In one place the slush had crystallised in circular patches—a type of pancake-ice." The wind and the motion of the water rounded off these minute pancakes in the usual way; "and in one case they had been rafted on to one another so as to appear apposed when viewed in section."

Without going further into detail, it may be stated that "pancake-ice" is the result of the sea freezing while rippled by the wind or disturbed by swell; on the contrary, "black-ice" (with its frequent accompaniment of "ice-flowers") is confined to still water. The term "pancake-ice" has a very definite and precise meaning; of all the terms used to describe ice, it is the one least liable to misconception. It would be well, nevertheless, to emphasise that, though outwardly the same, ice-pancakes may originate in two ways. Generally they form during the building up of young-ice, when wind and swell roughen the sea and prevent any widespread sheet being preserved. As such they range in size from 2 to 3 inches in diameter to floes 2 to 3 yards across, capable of supporting a sleeping seal. The other and the rarer type occurs during the decay of sea-ice, for the floes may then be broken into small areas and assume the form of pancakes; frequently, too, snow and slush, by the wearing down of the floes in summer or from the capsizing of an iceberg, collect in patches and by a to-and-fro motion behave like young-ice and form similar small pancakes.

*Horizontal Banding.*—A feature of young-ice, if it grew to any thickness, was the frequent presence of *horizontal banding*. Though previously noticed by DAVID and PRIESTLEY, this banded structure has never been closely examined and thoroughly explained. A block of young-ice of this nature was investigated in detail during the winter, and gave the following results:—

	Cl per cent.	Spec. Grav.
1½ cm. white opaque ice . . . . .	·274	·894
1½ cm. blue translucent ice . . . . .	·238	·918
3 cm. white opaque ice . . . . .	·212	·893
Thin blue translucent band (followed below by alternating narrow bands).	·207	·918

The Cl figures show that the difference between the two kinds of ice was not one of salinity; it is improbable, therefore, that it depends on the rate of freezing. The actual difference was one of density, the white bands being the lighter.

DAVID and PRIESTLEY say the cause is similar to what occurs in lake-ice, where during pauses in crystallisation large quantities of gas rise from decaying organic matter on the lake-bottom to the under surface of the ice. Some further explanation, however, appears necessary.

*Plasticity.*—The most striking physical character of young-ice is its plasticity. Pancake-ice, however, and ice formed from slush were never so plastic as black-ice, and this presumably was the result of their not being so salt. PETERSSON contends that plasticity is a peculiarity connected with the expanding properties of sea-ice down to about  $-20^{\circ}$  C. All varieties of ice are more or less plastic at their melting-point, but in the case of sea-ice, he says, the wide range of the eutectic points for the different salts in it virtually means that it has already partially begun to melt at  $-20^{\circ}$  C., and is therefore plastic from there up to the melting-point of the ice proper ( $-1.8^{\circ}$  C.).

*Chlorine Percentage.*—The saltiness of young-ice must depend partly on the rate at which it freezes; and possibly at this stage, when it is only 2 to 3 inches thick, the chlorine percentage may be an index to the total amount of included salt. The methods on the *Endurance*, however, allowed of the amount of chlorine only being determined. In young-ice about  $2\frac{1}{2}$  inches thick, it was on different occasions found to be present in the proportion of 7.23, 7.69, and 8.5 grms. per thousand. On the one occasion on which sea-water, over which ice was forming, was tested, the former contained 19.46 per thousand Cl, as against presumably 7 to 8 per thousand in the young-ice.\*

### III.—THE ICE IN MOTION.

Along the Antarctic coasts the rule seems to be for the sea-ice to be at all times liable to break up and drift away to the north and west. To this, however, there are two exceptions: firstly, where the configuration of the land is such as to shelter the ice from the prevailing winds, thus preventing disruption in winter, and sometimes even in summer; and secondly, where there are obstructions of the nature, for instance, of stranded bergs, which hold up the ice both in summer and in winter. The Weddell Sea fully bore out the general rule. At two places only is the ice at present known to be stationary; one of these is off Leopold Coast, where a chain of stranded bergs a little distance out from the land effectively anchors a long strip of ice and prevents it being continually subject to the restless motion of the pack; the other is on the coast of Graham Land between Ross Island and Joinville Peninsula, where, to judge by Ross's narrative and NORDENSKJÖLD's descriptions sixty years later, the ice very seldom breaks out. The former appears

\* These figures were determined by Mr JAMES, physicist to the Expedition, using what under the circumstances is the most convenient method, namely titration with silver nitrate. Unfortunately, no experiments were made to determine the specific gravity of ice as young as the above. The figures for specific gravity discussed later on were all got from ice over 2 feet thick, where the chlorine content only averaged about 2 to 3 per thousand, and was sometimes even less.

to be a case of fast-ice, and may possibly be a type of what DRYGALSKI calls "Schelfeis." Whatever the naming of this ice may be (it is best called "fast-ice" when anchored, "land-floes" or simply "heavy pack" when adrift), emphasis must be laid on its occurrence being merely a temporary interruption of the normal sea-ice cycle. Should such an interruption, however, persist so as to verge on permanency, then an important new feature is produced, namely a barrier (or, as NORDENSKJÖLD and others now call it, "shelf-ice"). Direct freezing from sea-water ceases, but the ice-mass continues to grow by the addition above of successive layers of snow, which in due course become névé. When the Weddell Sea becomes fully known, several barriers will probably appear on the map. Here reference need only be made to the one found by NORDENSKJÖLD in the north-east portion of the sea, namely along the Oscar Coast of Graham Land. In his own descriptions it is referred to as a "low ice-terrace"; but its height (30 metres) and the origin which he adopts for it make it quite comparable with the Great Ross Barrier; and it has therefore been proposed to call it in future the Nordenskjöld Barrier.

Where the ice is not in motion, therefore, fast-ice is developed, and, in extreme cases, barriers or shelf-ice. These are the exceptions; the rule is for sea-ice to be continually drifting. Bound up with the drift are the two related phenomena of cracks and pressure.

*Formation of Cracks.*—Cracks were partly the effect of the ice being in motion, but they were much more often the immediate factor allowing movement. There was always a tendency (which will be explained later) for an ice-field, whether of young-ice or of hummocky-pack, to have cracks formed across it. The smaller areas so formed then shifted their relative positions under the driving influence of the wind. Then either wide leads and lanes were formed, or, on the other hand, ice-raftering or even heavy pressure resulted. So it comes about that, although the formation of cracks gives rise to leads and lanes and therefore makes the pack navigable, yet these very openings may themselves enable pressure and hummocking to begin, with consequent danger and difficulty to a ship attempting the pack.

All cracks were a relief from strain, but the ultimate causes of the strain were very different, and in some cases unknown. In the Weddell Sea it was convenient to group the stresses as:—

- (i) Sudden differences of temperature—contraction cracks.
- (ii) Unequal loading—stress or strain cracks.
- (iii) Pressure.

The treatment of cracks of the last category will be deferred till pressure comes to be considered. Elsewhere in the Antarctic and in the Arctic similar types of crack appear to be the rule.

(i) Owing to the heavy autumnal snowfalls experienced by the *Endurance* in 1915, the underlying ice was almost everywhere protected from the effects of

sudden changes of temperature. Though some cracks, therefore, were possibly temperature cracks, they were never proved as such; and in the Weddell Sea, at any rate, they are not considered important.

Elsewhere in the Antarctic they apparently do occur, and in the Arctic, according to WEYPRECHT, their occurrence is extremely common. Since their formation, however, except at very low temperatures, has been called in question by PETERSSON, a detailed case must be mentioned. PRIESTLEY and DAVID describe how in the Ross Sea a crack formed with a fall of temperature from  $-16^{\circ}$  C. to  $-29^{\circ}$  C., and then opened and closed according as the temperature fell or rose. With the final rise of temperature to  $-18^{\circ}$  C. the young ice which had formed in the open water of the crack was overthrust a distance of 5 feet 6 inches. The importance of knowing the actual temperature comes in, in view of the remarkable conclusions arrived at experimentally by PETERSSON; for he illustrates by means of curves how, instead of being contracted by a fall of temperature, the volume of sea-ice increases down to  $-20^{\circ}$  C. Between  $-4.4^{\circ}$  C. and  $-6.4^{\circ}$  C., for instance, the ice he experimented with (comparable to frozen water of the open ocean) expanded its volume 0.002957. Figures such as these, he says, are only comparable to the changes of volume effected in a gaseous body. According to PETERSSON, therefore, sudden falls of temperature down to  $-20^{\circ}$  C. will not contract but will bend the ice upward and rupture it in that way. Many contraction cracks, however, such as that of PRIESTLEY and DAVID, are claimed at higher temperatures than  $-20^{\circ}$  C., and field experience, therefore, is so much at variance with laboratory experiment that the question must be left an open one.\* In any case, detailed descriptions of other temperature cracks are desirable, and PETERSSON'S experimental methods certainly want confirming.

(ii) For the second and by far the most important and commonest type of crack it has been hard to find an entirely suitable name, and, though the term "strain crack" has finally been adopted, it is realised that it is not an exact term, as all cracks are a relief from strain.

That the ice and its overlying load of snow were seldom in a state of equilibrium was a commonplace during all observations. The effect, for instance, of the irregular distribution of the snow-covering was always very noticeable, for there were even some places where the ice-surface was entirely below water. Consequently it is next to impossible to determine the specific gravity of sea-ice from the proportion above and below water-level; even in places bare of snow there must still be stresses of some sort. This seems obvious, and yet the specific gravity of sea-ice, as given in KRÜMMEL'S *Handbuch der Ozeanographie*, is based on just such unsuitable measurements as these made by MAKAROFF.

\* This discrepancy was pointed out to Mr PRIESTLEY in May 1919, who till then did not know of PETERSSON'S work. Although without access to his notes, he was most emphatic in saying that contraction cracks were possible with a fall of temperature not reaching so low as  $-20^{\circ}$  C. ( $-4^{\circ}$  F.).

WEYPRECHT gives a good instance to show how a patchwork field of pack-ice is always in a state of strain. He postulates the case of a floe 2 metres thick being divided by a crack, where young-ice immediately starts forming. It will soon be 1 metre thick, and by then the proportion above water should be 0.2 metre (taking 4:1 as the average proportion of submerged ice); but the thicker, earlier-formed ice bordering the crack has only increased perhaps one-tenth of this amount, and consequently in its case only a further 0.02 metre should emerge. So at the junction either the younger ice is held down below its proper level, or the older ice is buoyed up. In any case, there is a stress of some sort along the line of contact.

Sea-ice when newly formed is extremely plastic and can conform to such stresses as these; but as it ages it becomes much harder and less bendable, so that finally it must reach that state of strain at which it only requires some slight impulse to break it. In most cases this impulse will be the wind, though occasions must occur when the ice cracks simply because it has passed the breaking strain.

Proof of tension in a floe before it cracked was forthcoming in many ways: the ice-surface on one side of a freshly formed crack might immediately take a different level from that on the other side; the two sides might be displaced laterally; or, again, the opposite sides of a crack might open out at once to a breadth of some inches, to become stationary at that distance for a considerable time.

A special case of strain cracks, and one easily realised, occurs when a swell from the open sea runs under a wide ice-field. Over the trough of the wave, a thick ice-floe must be entirely unsupported; a crack parallel to the wave-front may result; when more than one such crack occurs, they will of course be parallel to each other. A case in point occurred on March 30, 1916. Whether when more than two in number they will be at equal distances apart is open to doubt; should it be so, the interval from crack to crack may possibly be half the wave-length. During the *Endurance* drift, never more than a couple of parallel cracks, originated beyond all doubt by a swell, were seen. This was probably due to the fact that, by the time the floes drifted into the region of swells from the open sea, they were already much reduced in size by the formation of ordinary strain cracks.

There were cases during the winter, however, when series of cracks formed whose relationship was so nearly parallel as to make one inclined to invoke the agency of a swell running under the pack from open water. The best of these cases was a series of four cracks (one of which ultimately developed into a lead) which opened on March 17, 1915 (fig. 3). Seven miles to the south-east there was open water on March 11, and beyond that open water as far as could be seen, perhaps even as far as Coats Land, thirty miles farther on. A swell was therefore well within the bounds of possibility. The cracks were not parallel, however, but seemed to form a fan-shaped group. This suggests another explanation, namely torsion.

If so, they belong to the third class of cracks, those due to heavy pressure. The detailed treatment of the latter, however, is best deferred until the phenomena of pressure have been discussed.

As a yet further case of specialised strain cracks, tide-cracks should be at least mentioned. The drift of the *Endurance* was never near enough the coast to enable them to be studied, but from published descriptions tide-cracks appear to be a perfectly normal result of strain.

*Pressure.*—When a moving ice-field became cut up by cracks running in different directions and many of them of considerable width, each floe as it was formed tended to travel at a different rate from that of the parent ice-field. A stretch of sea-ice was never a simple formation, but rather a great conglomeration of sheets

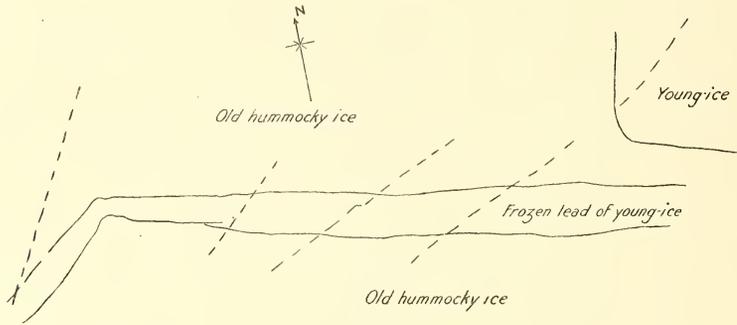


FIG. 3.

of young-ice and of floes which had survived the previous summer; consequently, each of the new areas detached from it had its own peculiarities of thickness, depth of snow, extent, and so on. As was shown above, it was these very peculiarities which produced the strains; and these in turn caused the cracks. They were also partly the cause of the different rates at which individual floes, formed from the break-up of an ice-field, travelled under the never-ceasing impulse of wind and current.

The main cause, however, of the different rates of travel was not so much the size and depth of the floes as the nature of their surface. Every hummock, in fact, acted as a sail, and the rate of movement therefore depended to a certain extent on the amount of hummocking in proportion to the area and weight of the floe. A legacy of previous pressure, these hummocks in turn became the cause of still further pressures. When two floes were moving at different rates, either the distance between them increased and a lead or lane passable for ships was formed, or the interval between floes decreased, one so to speak overtaking the other, and then the result, if there was sufficient momentum, was pressure in some form or other.

Very often there was first opening and then closing of the space between two floes. Take an imaginary case, namely an area which has been almost stationary: when movement starts the bigger floes will take some time to reach their proper speed; but, on the other hand, they will go on travelling after smaller floes have stopped moving. In the early stages, therefore, the big heavy floe will be attacked by smaller floes overtaking it; in the latter stages it itself will be the attacker of other smaller floes ahead; by reason of its size and weight it is pretty sure to take the upper hand whatever happens. Light pressure only may result, but, even so, it will only still further complicate the floe surface and create possibilities of yet further differences in speed.

Besides the forward motion imparted by the wind, there was also a swinging or turning tendency in almost every floe; this was either an effort to trim themselves to the wind, or the result of pressure from another floe; but, as the floes were continually hindered by each other, and the wind was not necessarily constant in direction, this swinging habit seemed to have no end. The process was of course more easily seen and realised when the pack was loose. For instance, on April 6, 1916, the floe on which the *Endurance* party was camped swung as much as  $180^\circ$  in one night; the ice at the time was described as being fairly open and travelling fast; but it was still open-pack, not drift-ice. When the ice was closer, the actual swinging was not so obvious, but the effects were greater; and one saw the type of pack produced which is so dangerous to sail through, and which the navigator calls "screwing pack."

The screwing or shearing habit resulted in pressure being located mainly at the jutting corners of floes. By one or other of the methods to be described, a hummock was formed of loose ice-blocks mixed up with a certain amount of snow; when movement ceased it settled downwards and became covered with falling and drifting snow, and in the end it would simply appear as a trifling inequality on the ice-surface, no bigger than a haycock.

Pressure worked in three ways:—

- (a) Bending;
- (b) Tenting;
- (c) Rafting.

These are the old terms given by early whalers and Arctic explorers, and are practically self-explanatory. Collectively, or when not particularised, the term generally used is "hummocking." Taken as a whole, hummocking resembled fairly closely the experiments which geologists make to illustrate mountain-building.

(a) Bending was characteristic of thin and very plastic ice. The most impressive result of this nature was the formation, in March 1915, of an arch 3 feet high and 8 feet span, formed of young-ice about 8 inches thick.

(b) Tenting was, on the other hand, confined to heavy floes, which being thicker

and less plastic were on that account less bendable; the ice swelled up, a crack formed perpendicular to the direction of the pressure, and a tent-like structure resulted. Other radiating cracks were usually developed; and, if movement continued, the blocks so formed were soon piled up into a pressure ridge.

(c) Rafting was the commonest of all the processes, and followed automatically when either of the other two methods already mentioned was carried to an extreme. Moreover, when rafting was going on, there was often a good deal of bending and tenting also taking place. In very thin ice, for instance, a process of rafting was developed in conjunction with bending, and gave a somewhat peculiar appearance to young newly-frozen leads, namely a series of lines at or nearly at right angles to the edge of the lead. This was due to the young-ice closing up when not more than 1 to 2 inches thick; the two sheets dovetailed into one another, like moving the fingers of one hand over those of the other, in such a way that the little finger of the right hand is above the little finger of the left, the third finger below, the middle above, the first below, and so on. The vertical grain of young-ice allowed of the process going on to a considerable distance, and in this way two sheets of young-ice might dovetail to a depth of 5 to 10 yards.

This was rafting at its very simplest. A slightly more advanced stage occurred where the screwing tendency brought jutting corner against corner, and forced one floe to override the other. Most impressive of all, however, was the formation of a great pressure ridge. Whether the work of a few hours, or a matter of days, it was the most forceful and exciting incident of life on the pack. One case is worth describing in detail; namely the occurrences in July 1915, which lasted for nearly a fortnight and exhibited in that time all possible types of "hummocking."

About 300 yards forward of the ship's bows a lead had formed in February 1915, and when frozen over with level young-ice had been found on that account the most convenient place on which to train the dog teams. By the latter half of March, however, a number of cracks had already formed across this lead (fig. 3), and their closing had led to a certain amount of light pressure. It was not, however, till July 14 and 15, as a result of a strong S.W. blizzard, that the topography ahead changed to any great extent. On these dates the floes broke up and re-arranged themselves; and in one case a small berg moved half a mile from its former position and swung round through 90 degrees. The result was that the ice-topography, with the exception of the 300 yards immediately ahead, was completely changed. It now consisted of islands of old pack-ice set among young-ice of two to three days' growth, the latter with a rough, uneven surface due to the overlapping of small pancakes. Pressure at this time, it should be noted, did not involve the older floes. For the next few days the ice was very restless, and the small berg already mentioned moved back very nearly to its former position relative to the ship, and at the same time swung a further 90 degrees.

The ice immediately surrounding the ship was in its component parts at least

over a year old; as floes and brash it had been the cause of the ship's being beset in January 1915, and it was cemented at that time into what may be termed an "ice-conglomerate." Its age and structure made it less liable to crack than young-ice, there being no vertical lines of weakness, so that a ship enclosed in such a position had all the appearance of security. Across this old ice to the frozen lead ahead a track ran from the ship for a distance of 300 yards, and was marked by cairns of ice-blocks, or pylons, as they were called.

On the 22nd of July heavy pressure was taking place beyond the farthest of these pylons, and it led to the destruction of a couple of places where the ice had been till then a subject of weekly investigation. The impact of the pressure caused a crack the same afternoon in the old-ice round the ship—a "shock crack," which ran parallel to and roughly 40 yards distant from the pylon road. On the 23rd pressure still went on, and a ridge was formed built up of the youngest ice. The old-ice, however, and the 3 feet thick young-ice formed since February had not begun to raft, though some more shock cracks were developed in both. On the 24th the pressure ridge had advanced another 10 yards over, but not involving, the 3 feet thick ice of February.

It was not, however, till the next day that the thicker ice, both that formed in February and that surviving from 1914, became involved. The already mentioned pressure ridge dating from the 22nd began an irresistible advance over the old-ice, weighing it down and breaking it up by means of "weight cracks." Though it was not really necessary, one almost felt impelled to walk fast or even to run in order to avoid the advancing pressure. On the 26th there was a respite, and any further movement took the form of shearing. Matters, in fact, remained quiet until the end of the month.

On the 1st of August, however, there being a strong S.S.W. blizzard blowing, new and unexpected developments took place. Not only did a crack form athwartships, running out at right angles to the ship on either beam, but a shock crack due to renewal of the July pressure started only 10 yards away on the starboard side. Working immediately set in along the latter crack, and blocks of ice 4 and 5 feet thick were soon involved in the pressure. The ship broke out of her ice-berth, and so rapidly did the shearing develop to starboard that it gave her the appearance of sailing over the top of the ice-floes. When in the afternoon things became quieter, the ship, instead of being safely bedded in an old conglomerate floe and 300 yards from the February lead ahead, found herself right in the middle of broken-up and unstable ice, where trouble might always occur.

This, however, was the end of the disturbances in the immediate neighbourhood, and the ship was once more frozen in, this time among a maze of hummocks and pressure ridges.

The tendency in the next two months was for the pack to become looser, and unfrozen pools and lanes were not infrequent in October. On October 15, by

means of one of these lanes, the ship moved to a new position 400 yards away, and was secured in a narrow lead not much more than the width of her beam. All would have been well had she not been warped round into a transverse crack four days later, for this move left her at the meeting-point of three floes. When pressure began again, instead of rising with it, she was twisted by the working of the three floes and developed a bad leak at the stern-post on October 24. No longer buoyant, she was now unable to weather such pressures as formerly would have given little trouble, and finally on October 27 she was abandoned, the bottom torn out of her and the water flush with the upper deck. She remained thus for a month, and it was not till November 21 that she finally sank under water.

A word may be said about *height of pressure ridges*, since there has always been a tendency to exaggerate this feature. During these fifteen months in the Weddell Sea it was quite exceptional for any ridges to be as much as 15 to 20 feet high; those of July and August 1915 were only 12 to 14 feet in height. On one occasion about three miles from the ship a hummock was found 25 to 30 feet high, built up entirely of blocks of sea-ice; it was not, however, part of a pressure ridge, but was simply an isolated hummock due probably to the encounter of two jutting corners. Again in March 1916, a thick slab of sea-ice was tilted up so that the upper edge was 25 feet above water-level; in this case at any rate it certainly was a jutting floe corner which had had to give way during screwing movement.

Accounts from the North have given the impression of extremely high pressure ridges in the Arctic seas. All these accounts, where reliable, are found to be based on phenomena seen north of Baffin Bay and Robeson Channel, where the land offers considerable obstruction to the drifting ice, and possibly causes higher ridges than on the open sea. NANSEN, on the contrary, definitely states that on the drift of the *Fram* across the North Polar Basin itself the highest hummock was 30 feet, and comparatively few exceeded 20 feet.

Should pressure ice, therefore, be met with in the South whose average is above 20 feet or even above 15 feet, it must point to the existence of land obstructing the free drift of the ice. A case in point was the belt of heavy hummocky-ice found by the *Endurance* on her southward voyage stretching from 70° S. 15° W. to 71° S. 22° W.; the floes were so close and heavy that it took six days to find a passage through. This very heavy ice was regarded as pointing to a deep embayment somewhere east of Coats Land, or at least to a very large ice-tongue protruding from the coast and so checking the westerly drift.

Pressure ridges were highest and most prominent when newly formed. They almost immediately sank to a position of equilibrium, as required by the specific gravity of the ice, the ratio of ice below to that above water being either 4 to 1 or 5 to 1. Possibly, as WEYPRECHT suggests, the supporting floes and pieces, which at least in the upper two-thirds were dry before the hummocking, when driven below became waterlogged and so lost some of their buoyancy. Whatever the cause, the

ridges certainly were less prominent in a few days, and soon lost their rawness and angularity by getting drifted over with snow.

*Formation of Cracks by Pressure.*—Two kinds were definitely established :—

- (a) Weight or hinge cracks.
- (b) Shock or concussion cracks.

Possibly there was a third, namely :—

- (c) Torsion cracks.

(a) Ice of advanced age was no longer plastic and did not bend, therefore, under the weight of a heavy pressure ridge piled on top of it, as it might once have done. The result, if the breaking strain was reached, was a longitudinal crack in front of the pressure, the ice being pressed down in much the same way that a door opens on its hinge (fig. 4). At the same time a number of radial cracks were developed; and the ice in front of the pressure was thus broken up beforehand into blocks of suitable size for further hummocking. Between a pressure ridge and a weight crack of

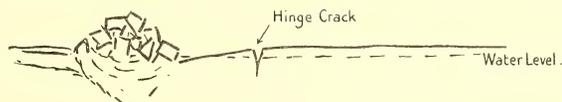


FIG. 4.

this nature the surface of the ice was often below the level of the sea; the pool formed, however, was apparently concentrated brine rather than sea-water.

(b) The shock or concussion crack, like the smaller radial cracks mentioned above, was also transverse to the advancing pressure ridge. It is sufficient to state that cracks of this nature were seen to form on many occasions (p. 811), and that the proximate cause was the impinging of one moving floe on to another relatively inert. Probably the development of the crack was made easier by the passive floe being already in a state of tension.

(c) All the above types of crack, whether due to outside causes (*i.e.* pressure) or to causes in the floe itself (*e.g.* stresses), were actually observed and are beyond all question. Torsion cracks are, however, more hypothetical. They have been discussed by ARCTOWSKI and HOBBS in an attempt to explain leads taking the form in ground-plan of a chain of pools. Citing DAUBREE'S well-known experiment on the production of two sets of cracks at or nearly at right angles, ARCTOWSKI makes the claim that the same thing may occur in an ice-mass relatively passive. On opening, a zigzag lead would result (fig. 5); and as it opens farther there would in the ideal case be a chain of diamond-shaped areas; but, as the effect in nature can hardly be as perfect as this, it resolves itself (so it is claimed) into a chain of pools. On one occasion a sketch was made of some opening cracks in the neighbourhood of the *Endurance* which seemed to be a case in point (fig. 6). The whole matter, however, requires

further observation, for other explanations are possible. Chains of pools, in fact, can be very easily accounted for by shearing and screwing.

*Effect of Wind on the Drift.*—During 1915 a drift indicator was set up on the floe about 50 yards from the ship; it was in no sense a current meter, but was an

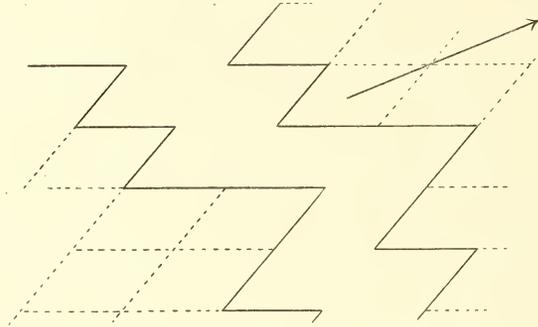


FIG. 5.

approximation to a drift meter, as it was ultimately possible to deduce the speed of the drift from the rapidity or otherwise with which the indicator reacted. It consisted of iron piping about 9 feet in length set inside a slightly shorter length of ship's rail. The latter was firmly fixed in the floe and was filled with a mixture of salt and

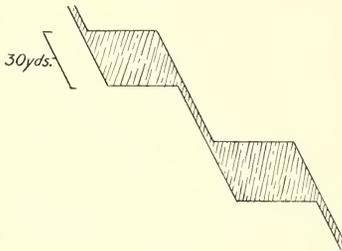


FIG. 6.

petroleum, so that there was very little chance of the inner piping becoming fast frozen. A vane had been fixed to the lower end of the piping, and an arrow-head at the upper end, in the same vertical plane as the vane. The arrow accordingly always pointed in the direction in which the floe was travelling.\* Commander WORSLEY made several observations daily, and at each observation rotated the arrow and the vane to  $90^\circ$ ; he then waited until they swung back, and the time which this took gave him a measure of the rate of drift. The result of these observations was to show that the floes always travelled with the wind, but slightly to the left. The velocity, however, did not depend entirely on the strength of the wind; it was influenced in great measure by the presence or absence of open water in the direction to which the ice was being taken, no matter how far off this open water might be.

M'CLINTOCK and later NANSEN have discussed the *right-hand* deflection in the Arctic. One case may be quoted to show the extent of the *left-hand* component in

\* Cf. E. H. SHACKLETON, *Heart of the Antarctic*, vol. ii, p. 413.

the Antarctic (fig. 7). From January 16 till January 22, 1916, a fierce blizzard blew for six days from S.W. by S. Despite this the floe on which the camp was situated drifted N. by E., *i.e.* two points more to the left than the wind. This was no doubt an extreme case; but it is worth noting that the trend of the Graham Land coast immediately to the west did not make things any easier for ice to move to the left.

The track of the ice-drift was influenced by three factors in all:—(a) the wind; (b) a left-hand component due to the earth's rotation; and (c) a true current. The unsolved problem is the amount and direction of the last factor in the Weddell Sea. NANSEN'S method might, however, be used, namely:—To lay off on squared paper lines representing the wind's direction and force at each observation (*i.e.* every four hours), the length of each line being proportional to the strength of the wind. When this is done an irregular track should result (not unlike the drift of the ice) which may cross itself at certain points. At these points, accordingly, the wind resultant for the period in question should be nil; the left-hand component should also be neutralised; and the distance, therefore, which the ship has travelled in the interval, as determined by observations, should be entirely due to the true current. The third factor should therefore be kept in mind when examining the drift chart of the *Endurance*. At first sight it looks as if wind were the only agent responsible, but it should not be forgotten that a true current, not determined as yet and perhaps only of limited extent, is quite within the bounds of possibility.

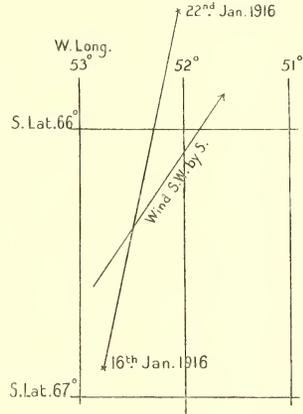


FIG. 7.

So far as drift control by wind went, it was possibly the result simply of 'long-shore winds. When one studies in this connection the *Deutschland* and *Endurance* tracks wherever they are near known coasts, it will be seen that the ships' tracks and the coast adjoining are approximately parallel. The abrupt change in the general direction of the two courses between 72° and 74° S. lat. may mean, therefore, that the coast of the unknown land to the south-west also shows a similar change in direction. It also makes it improbable that there is any strait separating Graham Land from the rest of Antarctica.

*Westerly Antarctic Drift.*—The most striking feature of the *Deutschland* drift, apart from the kink mentioned above, is the equally abrupt easterly deflection in 65° S., where the ice looks, indeed, as if it had come under the influence of the westerlies. This would be an unusually high latitude in which to meet the westerlies, and it is probable that there is some other reason for the behaviour here; for after a time the general direction of the *Deutschland* drift again becomes

northerly. Taken as a whole, the winds met with off the Antarctic coasts are southeasterly, with the result that the ice-pack moves towards the west. It has taken years for this fact to be properly appreciated; early circumnavigators, such as BRISCOE for instance, believed that the westerlies still prevailed far south, and sailed eastwards, not knowing how much they would have gained by adopting the exactly opposite course in high latitudes. The westerly drift round the Antarctic is well known to-day, and it is obvious that the course of future explorations will be very markedly influenced by this knowledge. It means, for instance, that the eastern borders of such seas as the Weddell Sea are free from ice, at least towards the end of the season, while on the west side the reverse is more likely. This makes it improbable, therefore, that the east coast of Graham Land will ever be charted from the sea, for it is unlikely that any ship will venture down the west side of the Weddell Sea, or having crept down Coats Land will risk penetrating farther northwest along the Wilhelm Barrier, with the ever-threatening possibility of being jammed against the land by pack from the east.

Graham Land obstructs the westerly drift; that and the low average wind-velocity in the Weddell Sea compared with the Ross Sea are the causes of the unusual congestion of ice which generally prevails in the former area. The *Endurance* tried to make its southing between 15° and 20° W. long., but from 60° onwards there was a continual struggle with the pack. There must, however, be an eastern limit to this ice congestion; possibly a ship sailing south along the Greenwich meridian may meet with no ice there even in January. One cannot say probably, for there is also the likelihood of a considerable indentation (and nourishing ground, therefore, for ice) into the continent between 15° E. and 15° W. long. The reason for supposing the existence of such a sea has already been referred to, namely the finding by the *Endurance* in 70° to 71° S. lat., 15° to 20° W. long., of a line of impenetrable hummocky pack heavier than anything encountered elsewhere, even off Graham Land. One felt compelled to think that it could only be due to the westerly drift piling up the ice either against a great ice-tongue (*e.g.* Termination Ice-Tongue in 100° E. long.) or along a N.-S. coast obstructing the normal drift. BELLINGSHAUSEN'S discovery of land in 69° S. lat., 16° E. long., marks the eastern limit of this possible indentation. A ship working westwards from Enderby Land would be taking the most suitable course for entering this presumed sea.

*Position of the Pack-Ice Edge.*—The course of future exploration is bound to be influenced to a great extent by the results of the voyage of the *Endurance*, for much that was formerly mere supposition in regard to the ice is now accomplished fact. It would also be most useful, therefore, if the average edge of the pack in the Weddell Sea could be determined from the records of all who have previously visited this region, and a chart drawn like that published annually for the Arctic by the Danish Meteorological Institute. An attempt was made to do so, but achieved only moderate success. The time does not seem suitable for it yet. In the first place,

there are hardly enough observations available, and such as there are, are for the most part valueless, owing to the observer seldom specifying in detail what type of ice he saw. For the present not much can be done to amplify the various pack-edges set down on the chart accompanying MILL'S *Siege of the South Pole* beyond adding the FILCHNER and SHACKLETON conditions. Such a map to be useful should, of course, have the day and month as well as the year inserted, as the edge is continually moving northwards. The only data as to the rate of this movement are supplied by the *Deutschland*, which drifted 6 sea-miles a day, and the *Endurance*, nearer the coast, which averaged 4 sea-miles a day.

#### IV.—CHANGES IN THE ICE.

From its very beginning the history of the pack-ice was one of continual, unceasing change. The field itself was never at rest. Driven by wind and current, it was cracked the one day, and compressed the next. Outwardly, therefore, it finally appeared very different from the original sheet of young-ice, which consisted either of black-ice covered with ice-flowers or of cemented pancakes. Its surface became a maze of hummocks and pressure ridges, for the most part drifted over with snow. These were the *outward* signs of change due to its being in motion; but *inwardly* the ice had also become very different, independently of whether it moved or not. It had altered in chemical constitution, in density, structure, hardness, elasticity, and so on. These changes, it should be noted, varied greatly according as the portion of ice examined was still floating in the water, or had been hummocked so as to lie above sea-level.

*Growth in Thickness.*—The rate at which undisturbed ice grew depended largely on whether there was a heavy snow-covering or not. Hence it could come about, and did, that the earliest-formed ice in the winter of 1915 was not necessarily the thickest at the close of the year. Observations on the thickness were made at several different points, but ultimately these became destroyed one by one, so that by October there was only one small area of 1915 ice whose entire history was definitely known. The final measurements for thickness were made here, and gave the result that by October 13 ice which started forming on February 6 was now 145 cm. (=4 ft. 9 in.) thick. This ice started forming in and about 77° S. lat.; and on October 13 the position was 69° 20' S. lat. Owing to the abandonment of the ship a fortnight later, this was the last measurement possible at this locality. It is more than probable, however, that the ice continued to increase in thickness until possibly the end of December, but certainly no later than this date. On plotting out the different measurements and continuing the diagrammatic curve so got in keeping with the composite curve of past observers, an additional 3 inches can be assumed. The maximum thickness of one-year ice in the Weddell Sea (except fast-ice in high latitudes) is therefore taken as 5 feet. Anything thicker than that is regarded with certainty either as having been rafted at some time or other, or as

being the result of two winters' freezing. Both these winters may have been spent as drifting pack-ice, or for the first of them the ice may have been held fast in some sheltered bay.

*Summary Table of Rate of Growth.*

Locality.	Date. 1915.	Thickness.	
		Inches.	Centimetres.
D	14th February	0	0
	16th February	6	15.25
	3rd March	12	30.5
	13th March	15	38.1
	6th April	21	53.4
	1st June	37.5	95.25
	6th July	40.35	102.5
F	6th February	0	0
	9th August	...	115
	7th September	...	136
	13th October	57	145
L	5th October	...	130
	10th October	...	131
	21st October	..	141

Certain floes, however, whose thickness was due entirely to freezing, exceeded 5 feet. Some of these were measured while still afloat, others immediately after being hummocked. A selection is given below of those of most interest, and from some of which important conclusions were drawn.

*Table of exceptionally Thick Floes due to Freezing.*

Date of Observation.	Thickness.	Remarks.
8th August 1915	145 cm.	Pressure ridge beside ship. The ice in which the ship was beset in January-February 1915. (80 cm. formed in 1914; 65 cm. formed in 1915, as proved by diatom layer.)
5th and 12th September 1915	7½ ft.	Part of a hummock. Diatoms were present only in the lowest part; presumed, therefore, to have formed almost entirely in 1914, and to have grown a few inches only in 1915.
8th December 1915	9-10 ft.	A slab in a hummock, not very far distant from the last locality.
31st December 1915	7 ft.	"Ocean Camp" floe.
7th February 1916	6 ft.	"Patience Camp" floe.
19th March 1916	6 ft. (approx.)	Portion of hummock nearly 25 ft. in height. Upper part made up of 2-3 ft. of "spotted ice" with diatoms at base, lower of 1-3 ft. of "fibrous ice" with current summer's diatoms at base.
30th March 1916	8 ft. 4 in.	"Patience Camp" floe. Less snow presumably than where measured on 7th February. Vertical lines pronounced from the very top downwards, <i>i.e.</i> all fibrous ice.

*Diatoms.*—In the summer countless diatoms made their appearance on the surface of the water, on the edges of the ice, and along its under surface; they inserted themselves between the plates and lived actually in the body of the ice itself. This may have been simply an effort to get to the light. At the end of summer, accordingly, a good number were entangled and became frozen into the ice, and so gave it a yellow colour. This discoloured band, therefore, marked the interval between two winter periods of freezing, and could be used as an index to the age of the floe. The piece of ice, for instance, noted on March 19 had two diatom layers; the second and lower was formed in summer 1915–16; the upper presumably in 1914–15; accordingly the uppermost (*i.e.* oldest) portion of the ice must have commenced freezing in winter 1914 at latest.

*Change in Structure.*—It had been well known to whalers for a long period that old hummocked ice could be used for drinking purposes; but this was knowledge which had apparently been lost, for the *Discovery* in 1901 melted snow for this purpose. It is an important point, however, in a ship's economy to realise the freshness of hummocked ice, as snow requires nearly double the amount of heat that ice does to produce a given quantity of water. The ice which was suitable for this purpose was very different in appearance from freshly formed young-ice with fibrous structure.\* It had become clear, almost transparent, had a conchoidal fracture, might almost be called blue in colour, and had a slightly spotted look. Though quite suitable for drinking, it was not entirely fresh; tested with silver nitrate, the solution always became cloudy, showing that some chlorine at least was still present. All the water used for chemical experiments on board the *Endurance* had to be distilled on this account.

This type of ice was apparently that examined by DRYGALSKI near the *Gauss* winter quarters in 1903, and by him called "Blaueis." He attributes the changes to the influence of wind and evaporation (*i.e.* ablation), basing his contention on the smoothed and rounded nature of the ice. That the latter appearance is due to ablation is certainly true, but that the change in structure is due to the same cause is unproved. The long imprisonment of the *Endurance* gave the opportunity for showing that the structural change was due to the high summer temperatures; it might partly take place in ice still afloat (*i.e.* not hummocked), but it reached its fullest development when the ice had been subjected to a summer's temperatures as a hummock above the water level.

About half the ice in the Weddell Sea was of this "spotted" nature (DRYGALSKI'S "Blaueis"). That the change was not due to wind follows from the fact that ablation, however important it may have been round the *Gauss* winter quarters, is nowhere known to be at all effective in the Weddell Sea. That it may play a part nearer the coast than the position of the *Endurance* is quite possible, but, so far as the

\* Called "fibrous" for convenience; young-ice is not really fibrous but platy in structure; the edges of the plates, however, give it a fibrous appearance.

measurements of ablation went, the results round the ship were nil. These measurements took the form of a marked stake embedded in the ice of some prominent hummock. One such was set up on May 21, 1915, and when examined for the last time on September 4, as on previous visits, it was found still crusted, like the ice around, by rime 1 inch thick. This was the rule everywhere throughout the winter.

In the summer, conditions were not quite the same, and changes did occur, but they were directly the outcome of the sun's heat. This was the very season during which quantitative measurements would have been of most value; but such were of course quite impossible after the ship was crushed in October 1915. The

summer changes are therefore the result of comparative observation, and quantitative tests are still required.

That the change from fibrous ice (*i.e.* striated ice showing vertical lines) to spotted ice can take place in hummocks is not new; the details of what takes place have been set down very clearly by HAMBERG. They amount to this: that the ice, when subjected to a temperature at and about the melting-point, loses some of the liquid salt inclusions, their place being taken apparently by air-bubbles; the ice then ceases to show its pronouncedly striated or fibrous appearance and becomes bubbly and almost granular.

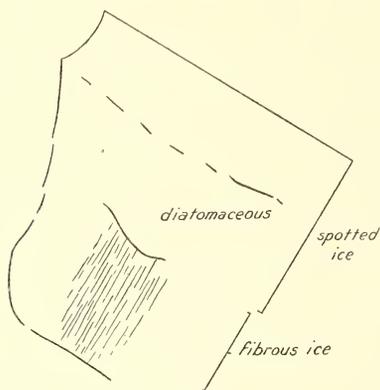


FIG. 8.

Traces, however, of the vertical lines can still be seen on very close examination and are a convincing proof of what has taken place. What had not been settled by Hamberg was the length of time necessary to effect this change. The length of life of the Weddell Sea floes being known, it can be definitely asserted now that the change can be effected in one summer.

One can also go further than this and say that the change may also commence while the floe is still in the water. In this connection the thick floes examined on August 8, 1915, and March 19, 1916, were of considerable value for what they told.

That examined on August 8, 1915, which is roughly sketched in fig. 8, was raised up into a pressure hummock on August 1; previously it formed part of an old floe which had lain ahead of the ship since very early in February 1915, and which was formed at that time by the cementing together of brash and ice pieces (dating from 1914) during the north-east blizzards of the latter part of January 1915. The upper portion, just over 80 cm. in thickness, was spotted

ice, and of this amount the bottom half was discoloured by diatoms. It was separated by a sharp line from 65 cm. of fibrous ice. From this specimen the following conclusions were drawn:—

- (1) The sharp line indicated a break in the freezing process during the summer 1914-15, and separated ice formed in 1915 from that formed the previous year.
- (2) The presence of diatoms showed that the ice was afloat in summer 1914-15.
- (3) It also showed that the ice must have been very loose to allow of these minute plants penetrating 40 cm. into the ice.
- (4) This in turn pointed to a temperature at or about the freezing point—just what was required to produce the structural change from fibrous to spotted.

The block examined on March 19, 1916, had been tilted up into a hummock a couple of days earlier. Its upper 2-3 feet consisted of spotted ice, in its lower portion discoloured by diatoms. The variation in thickness may have been partly due to summer melting in 1914-15; it resulted, at any rate, in an uneven boundary between the upper portion and the lower 1-3 feet of ice; the latter was also slightly spotted, but with the fibrous structure not yet entirely obliterated; in turn its lower layers also were strongly discoloured by diatoms. This was an important find, for it showed the effects by March of the summer heat of 1915-16; the change had already begun, but was not so far advanced as to obliterate entirely the fibrous structure. The arrival of diatoms seems to be the sign that the change is beginning.

The earliest date on which the structural change was definitely known to have commenced was on December 30, 1915. On that date a visit was made to one of the numerous areas of brownish-looking flat ice (the brown appearance was connected with a very thin snow-covering) and an attempt made to bore through the floe. Merely by working with the point of an ice-axe, it was soon possible, despite the water oozing up in the first few inches, to reach down 2 feet 6 inches. At one time it would have been impossible to have reached even a depth of 6 inches without excavating with a pick and shovel. The ice now was soft right through and through; and the whole ice-thickness must, therefore, have been practically at the melting-point.

On the same date, however, it should be noted that a floe with a 3-foot snow-covering was not so far advanced; for in this case it was only possible to work down a few inches with the point of the ice-axe. The snow-covering was now retarding rise of temperature, just as once it retarded freezing; this was evidence, therefore, of how the almost universal thick snow-covering on Weddell Sea floes worked towards prolonging their life.

*Physical Changes.*—The fracture and hardness of spotted ice are very different

from the same physical properties in fibrous ice. This was to be expected, and does not call for detailed mention.

Experiments were made from time to time to determine the specific gravity of the various types of sea-ice, and to discover especially if there was any relation between specific gravity and the amount of chlorine present. On the whole the results were not as satisfactory as they might have been, and, under the circumstances, were of course incomplete. There is good ground, however, for supposing that something may eventually be gained from them. The method used was that recommended by Mr JAMES, who himself made a good many of the determinations. The sample of ice was first of all weighed in air, in a temperature which varied from  $-4^{\circ}$  to  $-12^{\circ}$  C. (and which of course was not quite the same as that to which the ice had been exposed *in situ*); it was then weighed in paraffin whose specific gravity and coefficient of expansion were known; and the result calculated accordingly.

In a previous paper it was stated that the specific gravities of fibrous ice (*i.e.* ice showing vertical striæ) clustered round 0.92, whilst those of comparatively pure spotted ice were nearer 0.91. This was a somewhat hasty conclusion to draw from the results. At the time Dr OTTO PETERSSON'S paper "On the Properties of Water and Ice" had not come to notice. The very numerous references to contraction cracks in Polar literature made it appear that sea-ice below its freezing-point behaved like pure ice, and contracted on cooling—the exact opposite to PETERSSON'S conclusions. Inasmuch, therefore, as the determinations of specific gravity were made with the ice varying in temperature from  $-4^{\circ}$  to  $-12^{\circ}$  C., the possible expansion according to PETERSSON would be nearly 2 per cent., and all figures have, therefore, had to be re-examined. What has been done is to plot the specific gravity against the temperature of the ice at the time it was weighed. The result for fibrous ice shows a grouping of the values along lines which are perhaps comparable to PETERSSON'S curve. In the case of spotted ice, however, there are many serious discrepancies; but as this type contained considerably less salt than fibrous ice, it is quite natural to expect that its coefficient of expansion approximates rather to that of pure ice than to that of young-ice.

Leaving aside spotted ice, and considering only the platy or fibrous type, our measurements showed that its specific gravity was 0.92 at  $-4^{\circ}$  C. and 0.915 at  $-15^{\circ}$  C. The amount of chlorine present was about 3 per cent. These figures indicate the same order of things as PETERSSON puts forward, but of a very different magnitude. Between  $-4.4^{\circ}$  and  $-6.4^{\circ}$  C. he found an expansion of 0.002957 (*i.e.* more than three times the *Endurance* result) for ice of a kind which seems to be the same as the ice spoken of here as fibrous. The method used in the *Endurance*, however, was not sufficiently exact to merit more weight being attached to the results got by it than to Dr PETERSSON'S made in the laboratory. Even if they could be, any discrepancy could be easily explained by the fact that practically no two pieces of ice are identical.

Spotted ice has probably a lower specific gravity than fibrous ice, but the *Endurance* figures at any rate do not prove an invariable difference. They do prove, however, that KRÜMMEL's statement that sea-ice has a specific gravity of 0.92 in the Arctic and 0.95 in the Antarctic is quite untrue.

*Chemical Changes.*—The amount of chlorine present in the various ice-types was directly determined by titration with silver nitrate, Mr JAMES being responsible for the actual measurement. Results are given not as total salinities but in grammes Cl per 1000 c.c. of melted ice. This is made necessary by the fact that the amount of salt present relative to chlorine cannot be deduced by formula, as it can in the case of sea-water, but must vary, to what extent being at present unknown. To have determined the total salinity was quite out of the question on a non-oceanographical expedition.

The results showed that:—

- (1) The amount of chlorine initially enclosed (presumably in the form of brine) depended probably on the rate of growth—in other words, on the temperature at the time of formation.
- (2) Ice in the position of growth (*i.e.* unhummocked) slowly became fresher by losing its chlorine.
- (3) The chlorine was removed downwards and was not, as previously imagined, mainly pressed out on the surface. Just how this took place was not quite clear.
- (4) The loss of chlorine in winter was probably slow compared with that which took place in summer.
- (5) For ice to become drinkable, it required to be hummocked and exposed to a summer's high temperatures.

The most important data were obtained from three vertical pits put down in ice whose history was known and had been recorded. Those of September 7 and October 13, 1915, were put down in ice which commenced freezing and had gone on doing so uninterruptedly since February 6; samples of ice were taken every 20 cm., and examined for structure, salinity, and specific gravity. Those on September 7 showed invariably fibrous structure; those on October 13 (in ice of exactly the same history, the pit being only a couple of yards away), showed fibrous structure only in the lower two-thirds, for in the upper third there was also a tendency towards being spotted, which became very pronounced in the topmost sample. These series have been plotted diagrammatically, chlorine content increasing towards the right, and depth in the water downwards from the top of the page (fig. 9).

The third series, that of September 14, was collected from ice of a totally different history; the upper layers, formed in the winter of 1914, were spotted in structure and discoloured by diatoms; the middle portion was spotted, but vertical lines appeared on a sample being melted; and the bottom layers were pronouncedly

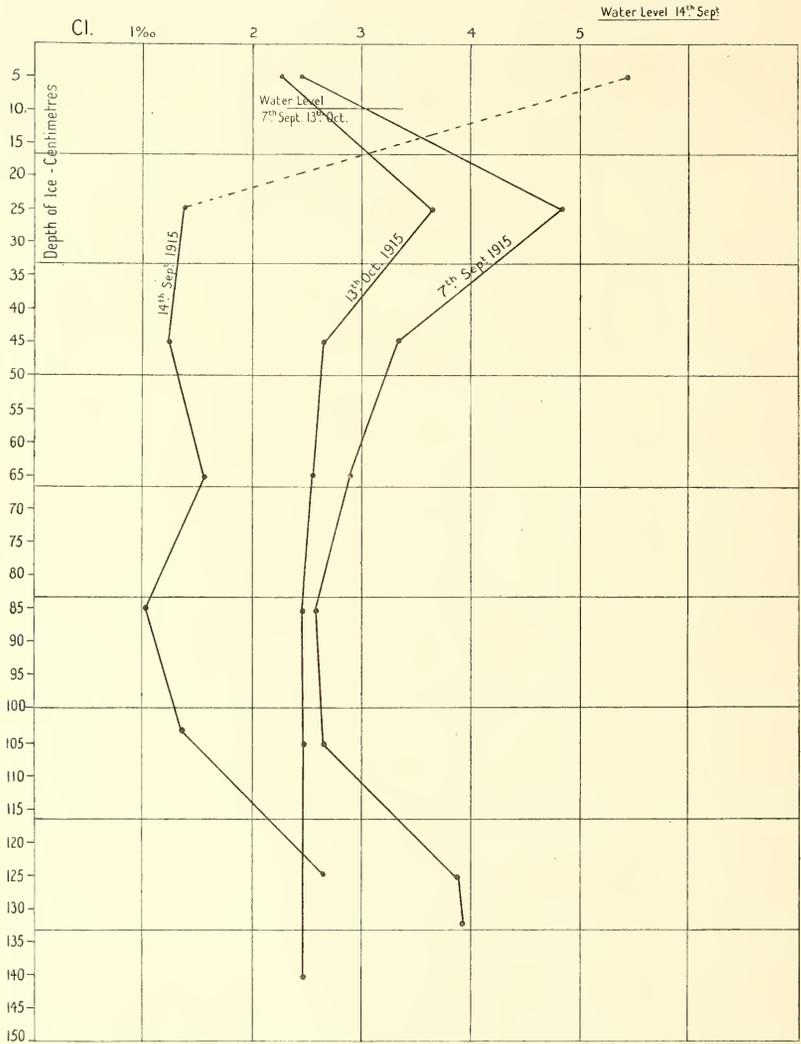


FIG. 9.

fibrous and were in fact simply young-ice. The spotted ice formed in 1914 or earlier is often referred to as old-ice; unlike young-ice, it had experienced high summer temperatures.

The two series in young-ice show how even in five weeks there has been a distinct freshening of the ice; in the case of the saltier layer (25 cm. down) the loss in chlorine amounts to 25 per cent. Layers less salt have not freshened in the same proportion. The curve has become smoother, and it looks on that account as if finally the amount of chlorine were going to be equally distributed through the ice, except perhaps in the very bottom layers where the ice is but newly formed.

The series in old-ice shows a freshening of the same order, but much more advanced. The very high chlorine percentage in the sample near the surface seems out of place: it is explained, however, by the upper surface of the ice at this point having been below water level, owing to its heavy load of snow; for in such cases salt water always seeped in laterally from the nearest crack and caused the upper layers of old spotted ice like this to appear even saltier than the young fibrous variety. The fact remains, however, that spotted ice as a rule is fresher than fibrous ice.

To summarise:—Young-ice had two possible lines of development open to it: either it remained floating in water or was hummocked. In both cases its structure became spotted instead of fibrous; in the case of hummocked ice, it also became translucent in appearance. The saltiness was appreciably lessened in ice afloat, but, if hummocked, the ice became fresh enough even for drinking purposes. That a little chlorine, however, was still present even then was proved by titration with silver nitrate.

#### V.—DECAY.

To the rule that Arctic and Antarctic pack are much the same there appears to be one noteworthy exception. In the matter of decay, sea-ice in the Antarctic, by all accounts, behaves very differently from that in the Arctic. It was a very rare thing, for instance, to see bare ice in the Weddell Sea, and when it did occur it was owing to the ice having formed late in spring and never having had an opportunity of getting covered by much snow. In no case was a pool of fresh water due to natural causes seen on the ice; salt pools certainly were seen, but they were all due to seepage of water into depressions caused by the weight of pressure ridges. Fresh-water pools, formed on camp sites owing to the amount of soot lying around on the snow, may be set aside as unnatural. Under exceptional conditions, however, fresh pools do occur in the Antarctic; NORDENSKJÖLD mentions having found them on the ice near Snow Hill Island, but gives no details; and they also occur in the Ross Sea in places where there is a good deal of dust scattered about over the ice.

In the Arctic affairs are very different, and melting of the snow to form fresh-water pools and lakes is extremely common, particularly in the American

Arctic Archipelago. NANSEN and WEYPRECHT both mention them as occurring in the neighbourhood of Franz Josef Land; the latter cites melting of the ice on the upper surface as the rule, and even maintains that this process may go on while the ice is still increasing by freezing on the lower surface. The evidence for this, however, was based on observations of the ice at the ship's stern, in the very place where abnormal conditions would be expected; practically no weight, therefore, can be given to WEYPRECHT'S statement that ice in northern latitudes melts about 1 metre on the surface each year.

Experience in the Weddell Sea makes it certain that there, at any rate, surface melting as a factor did not count. It must be regarded as abnormal. Except in summer there was no ablation, and even then it only affected the snow covering and not the ice beneath. The snow became granular and almost moist.

Other processes must be invoked to explain the decay, namely melting on the under surface and mechanical attrition. Probably there is little or no ice melted from below till the whole thickness reaches the melting-point. By all accounts, however, this is what happens in the Arctic; the diagrams obtained by plotting time against ice-thickness, based on the figures of the different expeditions, show at first a steep gradient until the thickness is about 8 inches; then a steady falling off in steepness, down to what appears to be the local average thickness; and then a line almost horizontal, until it *suddenly* steepens at the melting period. The steepness of the diagram at the melting period is ever so much greater than that at the initial freezing, indicating that the ice as a whole first reaches the melting-point and then melts practically all at once. On one occasion there was proof that this might happen in the Weddell Sea—on December 30, 1915, when it was possible to drive an ice-axe up to its head into the soft ice; but no large floe was ever actually seen to melt. Melting of this nature may be looked for, however, in sheltered bays, and is known to occur in the Ross Sea; but in the Antarctic ice-fringe as a whole the pack seems hardly ever to reach the melting stage until it has come under the influence of swells from the open sea.

In distinguishing drift-ice from pack-ice, it was pointed out that the former is opener and looser and moves faster accordingly; it lacks the inertia belonging to close-ice. This has a very important consequence, for it means that the outer edge is continually sealing off, so to speak, and the swell getting access to more extensive areas of ice than it would otherwise have operated on. The swell soon reduces the size of the floes, and this in turn helps on the formation of more drift-ice; and so on. Meantime, the movement of the floe up and down in the water is mechanically eroding the ice, apart from actual melting; melting alone would produce honey-combing, but this was a rare feature in the drift-ice fringing the pack; it looked, therefore, as if mechanical wear and tear was the most successful factor in producing decay.

In the case of the Weddell Sea ice, there was a local peculiarity, which must accelerate the break-up. In its progress north, the ice was being continually pressed against Graham Land and Joinville Island; S.E. winds accordingly had little effect in moving the ice, but S.W. ones drove it out towards the open sea; the former had a closing, the latter an opening effect. There was a point, however, where the ice *did* get away to the north-west, namely when it reached the latitude of Joinville Island. In the middle of March, 1916, in  $64^{\circ}$  S. lat., a south-easterly blizzard had practically no effect; in the beginning of April, in lat.  $62^{\circ} 30'$  S., a lighter wind from the same quarter drove the ice fast and far to the north-west. In this way separate areas are probably sliced off the main pack and driven into Bransfield Strait. There the noted currents of the Strait give it little peace, and it travels towards the South Orkneys often as fast as 20 miles a day. The *Endurance* party's experience of the current gave some idea of its force. From the 9th to the 12th of April the winds were easterly and east-north-easterly; and in this period during the daylight the boats were steered on a N.W. course; at night camp was generally made on a drifting floe. Observations on the 9th made the position  $61^{\circ} 56'$  S.,  $54^{\circ} 05'$  W.; but on the 12th showed the boats to be in  $62^{\circ} 15'$  S.,  $53^{\circ} 17'$  W.—a net loss of about 30 miles S.E. Dead reckoning, on the contrary, would have made the position at least 25 miles N.W. of that on the 9th, to say nothing of steady winds from E.N.E., which should have made it still farther west. These figures give an idea, though an inexact one, of the strength of the easterly running currents in Bransfield Strait.

To summarise what probably happens during the decay of the Weddell Sea ice:—The most important factor is the swell, which breaks down the floes, if not already in that condition, into smaller-sized pieces. Mechanical erosion then takes place by washing of sea-water against the ice. Finally, when the temperature allows of it, the ice-blocks are destroyed by melting. By the time that stage is reached, the ice is much comminuted, forming brash. The latter includes "bergy bits" (hummocked-ice finally taking this appearance) or "growlers," which are merely ice-fragments greenish in colour and so small that they hardly show above water. For several hours one morning the boats of the *Endurance* passed through a maze of bergy bits. At that time the ice was under the influence of the Bransfield Strait current; and this and the wind were carrying it, much battered and decayed, to its final melting-ground towards and beyond the South Orkneys.

The author wishes to take this opportunity of acknowledging his indebtedness to the Trustees of the Scott Polar Research Fund for the generous grants made by them to meet the expenses of printing this and a previous paper on "Depths and Deposits of the Weddell Sea."

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Mr J. M. WORDIE on "The Natural History of Pack-Ice as observed in the Weddell Sea."—PLATE I.



*Field-Ice.* A field of hummocky pack reaching to the horizon.



*Field-Ice.* Mainly hummocky pack ; in the middle distance a frozen lead of young-ice.



Mr J. M. WORDIE on "The Natural History of Pack-Ice as observed in the Weddell Sea."—PLATE II.



*Close-Pack.* Ship's progress stopped. Only a few patches of water left between the floes.



*Close-Pack.* Ship steaming through large floe of very thin young-ice.



Mr J. M. WORDIE on "The Natural History of Pack-Ice as observed in the Weddell Sea."—PLATE III.



*Open-Pack.* Floes hummocked, but sufficiently light to be broken by ship charging.



*Drift-Ice.* Floes moderately light.



Mr J. M. WORDIE on "The Natural History of Pack-Ice as observed in the Weddell Sea."—PLATE IV.



*Pressure Ridge.* Hummocking of young-ice; in foreground, still younger ice covered by ice-flowers.



*Ice-Flowers.* Detail of crystals.



XXXII.—On Old Red Sandstone Plants showing Structure, from the Rhynie Chert Bed, Aberdeenshire. Part IV. Restorations of the Vascular Cryptogams, and Discussion of their bearing on the General Morphology of the Pteridophyta and the Origin of the Organisation of Land-Plants. By R. Kidston, LL.D., D.Sc., F.R.S., and W. H. Lang, D.Sc., F.R.S., Barker Professor of Cryptogamic Botany in the University of Manchester. (With Five Plates.)

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This part of the account of our examination of the plants preserved in the silicified peat-bed of early Old Red Sandstone age found at Rhynie will be devoted to the consideration of a number of general questions concerning the four Vascular Cryptogams which it has yielded.

1. In the first place the morphological characters of *Rhynia Gwynne-Vaughani*, *R. major*, *Hornea*, and *Asteroxylon* will be reviewed and the attempt made to reconstruct the external appearance of these plants as they grew. In relation to this a few additional features of the plants will be described.

2. This will lead naturally to a consideration of the general bearings upon plant-morphology of the facts mentioned in this series of papers.

#### RECONSTRUCTIONS OF THE EXTERNAL MORPHOLOGY OF THE VASCULAR PLANTS OF THE RHYNIE DEPOSIT.

The structure of the various parts of the four Vascular Cryptogams found in the Rhynie peat-bed has been described in the three preceding Memoirs of this series.\* In each case proofs or indications of the connection of the parts have been mentioned and discussed. The chief features are summarised in the diagnoses of *Rhynia Gwynne-Vaughani*, *Rhynia major*, and *Hornea Lignieri* in Part II, and of *Asteroxylon Mackiei* in Part III; these descriptions need not be repeated.

The reconstructions on Pls. I and II represent our conception of the external form and relative sizes of the four plants. The absence of specimens preserved as impressions necessitate such reconstructions being to a certain extent imaginative. This especially applies to the more complex plant of *Asteroxylon*. Even for this, however, and certainly in the cases of the simply constructed sporophytes of the Rhyniaceæ, the reconstructions probably give a fairly correct idea of the habit of the plants.

The brief notes that follow will serve to indicate both those features in the reconstructions for which we possess clear and direct evidence, and those which have to be supplied more or less conjecturally. The opportunity will be taken to add

\* *Trans. Roy. Soc. Edin.*, vol. li, p. 761; vol. lii, pp. 603, 643.

some new facts regarding the various plants which have come to light since the descriptions were published.

*Rhynia Gwynne-Vaughani* (Pl. I, fig. 1).

We have some direct evidence as to the mode of growth, height, and general habit of this plant. The block represented in Part I, fig. 5, in which the plants were preserved standing erect as they grew, shows the crowded, rush-like growth of the erect, tapering stems. These could be traced for a length of 13 cm., but were incomplete. In the reconstruction the plant is represented as about 17 cm. high, which may fairly be taken as about the mean height. Since, however, stems have been met with of 3 mm. diameter, while the stems in the specimen in Part I, fig. 5, were of the more usual diameter of 2 mm., the plants of *Rhynia Gwynne-Vaughani* probably attained a somewhat greater height than is shown in the reconstruction; a height of 20 cm. was suggested in the diagnosis.

The aerial stems tapered from a diameter of two (to three) millimetres at the base to about one millimetre. Examples of dichotomous branching have been met with sparingly. We have represented the sporangia as terminating some of the tapering stems, and take the size of the sporangia, from the few specimens seen, as about 3 mm. (or slightly more) in length by 1 to 1.5 mm. across. The rhizomes, of which only a few good specimens have been seen, were stem-like and about the same diameter as the aerial stems; they bore rhizoids on the lower side.

Most specimens of *Rhynia Gwynne-Vaughani* have shown the structures which we have spoken of as hemispherical projections. The size and distribution of these are best shown in figs. 7 and 8 of Part I; these represent pieces of stem, about 5 mm. in length, and bear on the surface turned towards the observer five and three projections respectively; there are no projections on the piece of stem in fig. 6. The projections are somewhat longer in the direction of the length of the stem, and have thus an oval outline; they are about  $\frac{1}{3}$  mm. long. These projections are simply indicated by dots in the reconstruction. The larger or smaller adventitious branches, which occupied the position of some of the hemispherical projections, are also represented in this.

Some further particulars with regard to the hemispherical projections may conveniently be given here. Their general structure was illustrated in Part I, figs. 50 and 51. It was there shown that the projection is a localised protuberance of small cells referable to divisions in the epidermis and the layers immediately below this, and bursting the thick cuticle. Both a vertical elongation of the cells and their septation by thin walls are concerned in the localised growth. A similar longitudinal vertical section of another projection is given here (Pl. III, fig. 5).

To this we have now to add the fact that in a number of examples the projection has been clearly seen to have formed more or less directly underneath a stoma.

Whether this can be assumed to hold generally is, of course, not established, but may be regarded as probable.

A good example is represented in figs. 6-8. As the general low-power view (fig. 6) shows, the plane of section has passed tangentially to a stem of *Rhynia Gwynne-Vaughani*. A portion of the stem bears two hemispherical projections cut in oblique tangential section and in part seen from the outer surface. Continuing the line of the stem, another hemispherical projection that was evidently borne on the same surface has been shaved off by the section and is viewed directly from above. The two portions are more highly magnified in figs. 7 and 8. A stoma (s.) is seen clearly in relation to the lower of the attached projections in fig. 7, while the position of the stoma is indicated by a dark patch on the surface of the other projection. The stoma (s.) is seen quite clearly on the isolated projection in fig. 8. A number of examples similar to this have been observed, and in them also the position of the stoma was near one end of the oval projection. Whether this was the end directed towards the base or apex of the plant is uncertain. The additional example in fig. 9 shows the stoma (s.) at one end of a small projection, apparently in an early stage of development.

In the light of these specimens it is clear that the hemispherical projections cannot be regarded as part of the primary construction of the plant as at first developed.

Many of the hemispherical projections did not undergo further development or change. What appears to have been an exudation, in which fungi often grew, sometimes formed to the outside of the projection as the stems lay in the matrix. In other cases the projections were the seat of further developments. A single specimen has been seen in which a projection, prolonged vertically from the surface, resembles an emergence (Pl. III, fig. 10). Sometimes their superficial cells grew out as rhizoids (Part I, figs. 52-54). At other times growth resulted in the development of lateral, adventitious branches; these in some cases remained small, and may have fallen off and served as a means of vegetative reproduction; often, however, they were larger and more strongly attached, though their vascular system was separate from that of the stem bearing them (Part I, figs. 55-60).

Comparisons of the peculiar hemispherical projections on the stems of *Rhynia Gwynne-Vaughani* are possible both with normal and pathological developments in recent plants.

They show certain resemblances to lenticels which, when formed in relation to the original surface of a stem, usually develop below the stomata. Nothing in the details of structure of the hemispherical projections of *Rhynia* indicates, however, that they were related to normal gaseous exchange. This comparison is thus not a very close one.

A more suggestive comparison is with certain intumescences that form on the stems and leaves of various plants, either as a result of the excessive moisture of

the atmosphere, or of the presence in this of injurious vapours. Numerous examples of such intumescences are given in works on plant-pathology.\* Perhaps the most striking figures for comparison are the photographs of intumescences † formed beneath the open stomata of leaves of cauliflower, etc., as a result of the entry of dilute vapour of ammonia. The elongation of the affected cells at right angles to the surface, and their subdivision by thin walls in the intumescences, present a remarkable similarity to the changes which result in the hemispherical projections of *Rhynia*.

There are no close comparisons to advance for the production of definite organs as new growths from intumescences. The tissue composing the latter does not, however, differ profoundly from callus, which, as is well known, is often the seat of adventitious growths.

In connection with the hemispherical projections and adventitious branches of the stems of *Rhynia Gwynne-Vaughani* another feature which is clearly pathological must be briefly described. A considerable number of the stems show dark necrosed areas extending more or less deeply from the epidermis; in other specimens the dark necrosed mass is wanting or has more or less completely disappeared leaving a larger or smaller cavity. Examples of these appearances are shown in figs. 11-14. In some cases the necrosed area appears to be related to the place of detachment of an adventitious branch (Part I, fig. 55), and sometimes it corresponds to the position of a hemispherical projection. Often, however, no such relation is to be traced. The necrosis cannot be proved to be related to the position of a stoma, though this possibility is by no means excluded. There is no evidence that the necrosis is caused by the presence of fungi; fungal invasion may be extensive without any signs of necrosis. Fungal filaments and other organisms may, of course, be present in the resulting cavities.

The feature of special interest is the behaviour of the cells abutting on the necrosed area or bounding the cavity. As shown in figs. 12-16, they had undergone changes that must have taken place during the life of the tissues. The cells are often elongated at right angles to the dead tissue of the cavity, and frequently show evidence, by the presence of thin walls, of an active cell-division that can without doubt be interpreted as a reaction to the wound. The arrangement of the cells and the mode of growth of the tissue resembles what is found in the formation of the hemispherical projections.

The further interest of these peculiarities of the remains of *Rhynia Gwynne-Vaughani* will be considered in the section of Part V dealing with the conditions of accumulation and preservation of the deposit.

\* Cf. SORAUER, *Pflanzenkrankheiten*, Aufl. 3, Bd. 1, p. 435 ff. KUSTER, *Pathologische Pflanzenanatomie*, Aufl. 2, p. 44 ff.

† ERWIN F. SMITH, "Mechanism of Tumor Growth in Crown Gall," *Jour. Agric. Res. (Washington)*, vol. viii, pl. 60, etc.

*Rhynia major* (Pl. I, fig. 2).

In the case of this plant there is no direct indication as to height or habit. All parts of the plant, however, are known and are distinctly larger than the corresponding parts of *Rhynia Gwynne-Vaughani*. The diameter of the cylindrical stems ranged from 5 or 6 mm. to under 1.5 mm. The stems are known to have branched dichotomously, and doubtless tapered as in the case of the smaller species. In the reconstruction we have represented the plant as about three times the height of *R. Gwynne-Vaughani*. The sporangia are known to have terminated some of the slender axes about 1.5 to 2 mm. in diameter. They attained the large size of 12 mm. × 4 mm. Sometimes two sporangia lay side by side in the peat as if they had terminated two branches resulting from a dichotomy. Hemispherical projections and adventitious branches are not known to occur in this species. The most satisfactory specimens of rhizomes *in situ* (Part I, fig. 13) show that they grew horizontally and were cylindrical, stem-like, and dichotomously branched. They bore rhizoids on the lower surface, sometimes on large bulges. The features thus briefly touched upon will be found expressed in the reconstruction.

We have little to add to the description of this species, but the opportunity may be taken to figure an obliquely longitudinal section of the apical region of a branch (Pl. IV, figs. 17 and 18). The actual apical meristem is contracted and collapsed, but the progressive enlargement and elongation of the cells behind this can be traced. The fact that the layer of cells with dark contents just below the outer cortex can be traced near to, but not up to, the apex is of interest (fig. 17).

As pointed out above, hemispherical projections like those of *Rhynia Gwynne-Vaughani* have not been found in *R. major*. Further, while the stems of the latter plant may be very perfectly preserved or badly decayed, they do not so commonly exhibit the wound-reactions around cavities due to necrosis described for *R. Gwynne-Vaughani*. Examples of necrosed areas and of wound-reactions that must have taken place during life have, however, been met with. This is shown in a very striking fashion by the two stems represented in fig. 19 on Pl. IV. In the case of the stem on the left, the cortical tissue had disappeared from a sector of the stem as seen in transverse section. Regenerative activity involving enlargement and division of the cells thus exposed had taken place. This proceeded both from cells of the cortex and of the phloem (fig. 20). In the other stem there was no cavity, but the region of cortex below and around a dark necrosed patch had been the seat of enlargement and division of cells. It contrasts with the normal cortex in the arrangement of the groups of newly formed cells and the whole character of the tissue. A portion of the disturbed growth in the neighbourhood of the stele of this stem is shown more highly magnified in fig. 21.

The enlargement of the cells that here precedes their division can be compared with another appearance represented in fig. 22 for *R. major*. In the case of this

stem certain of the cortical cells at two or three regions of the transverse section are markedly enlarged as compared with the others that are of normal size. A similar appearance was recorded for a stem of *R. Gwynne-Vaughani* in Part I (p. 770, fig. 74).

This feature, like the wound-reactions, suggests comparison with a reaction of the living plant to some prolonged stimulation.

*Hornea Lignieri* (Pl. II, fig. 3).

For this plant also we have only the fragmentary remains of all the parts and no specimens to show the general habit or height. It has been represented as somewhat smaller than *Rhynia Gwynne-Vaughani* since its stems did not, on the whole, attain the diameter of those of the latter plant, and also give the impression of having been less rigid.

The reconstruction shows the tuberous lobes of the rhizome from which the erect stems arise. These were repeatedly branched dichotomously. Some of the finer branches terminate in the sporangia, which were considerably smaller than those of *Rhynia Gwynne-Vaughani*. The sporangia may stand singly or in pairs, or may themselves be actually involved in the dichotomy of the branch-apex which has produced them, and therefore appear lobed.

We have no further facts to add to the description of *Hornea* given in Part II.

*Asteroxylon Mackiei* (Pl. II, fig. 4).

Since *Asteroxylon* was a much more complex plant than *Rhynia* or *Hornea*, the reconstruction of its general external appearance from the fragmentary remains is more difficult, although there is evidence for most of the parts represented in the reconstruction. It has, however, been found necessary to infer the relative proportions and connection of the parts in forming a representation of the whole plant.

Mention may first be made of features regarding which evidence will be found in the description of *Asteroxylon* in Part III. The existence of a dichotomously branched, leafless rhizome without absorbent hairs was fully established. Certain finer root-like branches of this were found to penetrate fragments of plants in the peat. A gradual passage from the leafless rhizome into the stem, which became clothed with small simple leaves, was also demonstrated; in the intermediate, transition region the leaves make their appearance as small scales. The occasional, dichotomous branching of large leafy shoots was met with, but this contrasted with the predominantly lateral relation of the branches on most main axes. In the case of the lateral branches and the finer ramification of the plant, dichotomous branching appeared to be more probable. The leaves on the main stems and branches were closely crowded and attained a length of over 5 mm. The shoot must have had much the same appearance as that of various species of *Lycopodium*.

In the impressions of *Thursophyton* (*Lycopodites*) *Milleri*, a plant of the Middle Old Red Sandstone flora of Scotland, which also occurs in Norway, we have a similar general habit to what is here assumed for the leafy shoots of *Asteroxylon*.

The repeatedly dichotomous leafless branches, which are believed to have borne the dehiscient sporangia, are represented in the reconstruction as the fertile region of the plant. Since, however, the connection of these structures with the vegetative organs of *Asteroxylon* is not established, a break is left in the restoration at this point.

It is with regard to the general habit of the plant as a whole that direct evidence is lacking. We have met with nothing pointing to the branched leafy shoots having been horizontal or prostrate, and have therefore represented them as erect. The transition from the leafless rhizome to the base of the leafy shoot also appears to have stood vertically. In order to connect these parts naturally, we have assumed the existence of a more or less horizontal branched rhizome, giving off, on the one hand, downwardly growing root-like branches, and, on the other, erect leafy shoots. This assumption seems natural and justified in the light of our knowledge of the mode of growth of other plants with somewhat similar characters (e.g. *Psilotum* and various species of *Lycopodium*).

It is further supported by the large specimen of a rhizome of *Asteroxylon* represented in fig. 24 on Pl. V. This specimen dips downwards and penetrates a large stem of the plant lying in the peat. The basal region of the rhizome is of interest since it has a well-marked epidermis and bears a number of scale leaves; this region has the structure intermediate between a leafy shoot and a rhizome. On tracing it on to the more distal portion the well-defined surface is lost and the structure is that typical of the rhizomes of *Asteroxylon*. This specimen thus affords proof of the direct passage from a leaf-bearing axis into a rhizome, while the transition from a rhizome to a leafy shoot was followed in Part III (p. 647 ff.). Fig. 23 on Pl. IV is a photograph of a portion of epidermis of a stem of *Asteroxylon* in surface view. It shows the median line or ridge on the outer wall of each of the epidermal cells; this feature of *Asteroxylon* was recorded on p. 653 of Part III, but not figured. The similarity in this detail of structure between *Asteroxylon* and *Rhynia Gwynne-Vaughani* will be evident if fig. 23 is compared with fig. 31 of Part I.

The remaining figures on Pl. V are from a series of transverse sections cut through the terminal region of a small leafy shoot of *Asteroxylon*. The crowded tips of the leaves were noticed at the surface of a block of the chert and a complete series of nine sections prepared in the hope of obtaining the actual growing point. Unfortunately the apical meristem itself was ground away in the process of cutting; it came between the second (fig. 25) and third (fig. 26) sections of the series. Fig. 25 shows a complete and almost perfectly transverse section of the bud just above the growing point. The leaves of the bud arranged in a complex spiral (much as in a corresponding section of *Lycopodium Selago*) diminish in size on passing

inwards towards the centre. The next section, represented in fig. 26 and more highly magnified in fig. 27, passed through the tip of the stem below the growing point; it was so close to the latter that the widening of the stem leads to the superficial tissues being cut somewhat tangentially. Epidermis (*ep.*), outer cortex (*o.c.*), and the outer zone of the inner cortex (*i.c.o.*) can be distinguished in order, although the cortical tissues are not completely differentiated. The condition of the middle trabecular zone of the inner cortex (*i.c.m.*) is of interest. The trabecular structure is clearly marked, but the radial depth of the zone is short. The inner zone of the inner cortex (*i.c.i.*) is of full width, and its rather imperfectly preserved tissue passes without a sharp limit into the stele.

In the stele the xylem (*x.*) forming the forked poles of what would become the stellate xylem is alone differentiated, there being no tracheides developed in the central connecting portion. Leaf-traces (*l.t.*) departing from the poles of the stele are seen around the latter. The soft tissues of the stele are preserved, though somewhat imperfectly. It is clear from this section that the poles of the stelar xylem were differentiated close behind the apical meristem.

The other sections of this series show that the central portion of the stelar xylem did not become differentiated for some distance behind the apex. A stele from the middle of the series is represented in fig. 28, the lowest section of the series is shown complete in fig. 29 and its stele more highly magnified in fig. 30. This lowest section shows that at the base of the series the differentiation of the stelar xylem was hardly further advanced than in figs. 26 and 27, although a few elements of the connecting metaxylem can be recognised. The outer cortex has attained the structure found in mature stems; the tissues of the inner cortex are too poorly preserved and crushed to be instructive.

This complete series confirms and extends the information as to the arrangement of the leaves in the bud shown in Part III, Pl. V, fig. 36, and as to the structure of the stele with its xylem imperfectly differentiated shown in Part III, Pl. VIII, figs. 59, 60. The series affords conclusive evidence that the general differentiation of the stellate xylem of the shoots of *Asteroxylon* was centripetal; the position of the protoxylem in the ends of the rays was shown in Part III to be as a rule enclosed or mesarch.

#### SOME BEARINGS OF THE RHYNIE PLANTS ON THE GENERAL MORPHOLOGY OF THE PTERIDOPHYTA AND THE ORIGIN OF THE ORGANISATION OF LAND-PLANTS.

The deposit at Rhynie gives us a remarkable glimpse of the vegetation of the Early Devonian\* period. The four higher plants, which are all Vascular Cryptogams, have the double interest of being the most simply organised Pteridophyta known and of being the most ancient fully-known forms of this group. In relation to the

\* The term Early Devonian is here used to include the period represented by the Lower and Middle Old Red Sandstone, but to exclude the Upper Old Red Sandstone.

descriptions of the plants in the three preceding papers of this series, comparisons have been made with existing and extinct plants, and some theoretical aspects of the facts have been indicated. Although this course involves a little repetition, some of the general bearings of these plants on the problem of the origin of the morphological construction of land-plants must now be considered.

As regards the origin of the type of alternation of generations and the balance of the sexual and spore-bearing stages in the life-history, the Rhyinie plants give no information. The plants known to us were clearly the sporophyte generation. The development of the spores in tetrads similar to those of other Vascular Cryptogams points clearly to the existence of a sexual generation or gametophyte. Of the nature of this we have no evidence. The absence of evidence is so far in favour of the gametophyte having been much simpler and more delicate than the sporophyte, as is the case in all the Vascular Cryptogams the life-history of which is fully known.

It is on the organisation of the sporophyte in the Vascular Cryptogams that most light is thrown by the Rhyinie plants. Apart from questions of physiological morphology, with which we are not here concerned, this is a comparative and historical problem. The historical data are necessarily imperfect, and their lack has led to much speculation of doubtful value, although opposed speculations have served to define aspects of the problem. It is in the additions they make to the ascertained historical data that the great importance of the Rhyinie plants consists. Without entering fully into speculations on the origin of the Pteridophyta and their characteristic organisation, it will be necessary to set the new facts in relation to them.

Existing Vascular Cryptogams may be broadly said to present us with a few main types of organisation of the sporophyte. These are the Fern type, the Equisetum type, the Lycopod type, and the type of the Psilotaceæ. The general characteristics of these are familiar and need not be stated. It is only necessary to direct attention to the facts that all these types agree in having shoots composed of stem and leaves, and that in all, except the Psilotaceæ, the plant-body has definitely characterised roots. In the Psilotaceæ roots are wanting, the aerial stems, with their smaller or larger leaves, arising from a system of leafless rhizomes clothed with absorbent hairs.

The extinct Pteridophyta of earlier vegetations, back to and including the Carboniferous and Upper Devonian periods, add, so far as we know, no essentially different types of organisation. They make us acquainted with varied and interesting forms of the Fern, Lycopod, and Equisetum types, and they add the wholly extinct type of the Sphenophyllales. The vegetative body of all these plants is, however, composed of root, stem, and leaf, and the comparison of the plants known from the Upper Devonian to the existing period does not throw light on the origin of this prevailing differentiation of the plant-body.

Even before the discovery of the material described in this series of papers interest was naturally focussed on the plant-remains earlier than the Upper Devonian. These were always incomplete, a serious drawback in making comparisons, but on

the whole indicated plants of more primitive organisation than those known from the Upper Devonian onwards. Without entering into an enumeration or survey of these Early Devonian plants from Scotland, Norway, Canada, Bohemia, and elsewhere, some of their features may be mentioned. In many of them the stems bore more or less evident and usually relatively small leaves, while others resembled fern-fronds without laminae. The appearance of most of the Middle Devonian plants was such as to show that a distinction of stem and leaf had been established at that period. On the other hand such plants as *Pseudosporochneus*, and especially the Lower Devonian *Arthrostigma* and *Psilophyton*, strongly suggested an even more primitive organisation on the whole. Many of these remains, though now clearly shown to have been vascular land-plants, have at various times been regarded as Algæ. Other anomalous plants of the same period still imperfectly known may not improbably find their place in this latter group, or may have combined characters that are now distinctive of Algæ and Pteridophyta.

These indications of plants of simpler and more archaic organisation than any Vascular Cryptogams of later periods, and the consequent interest of the Early Devonian period for the study of early steps in the land-sporophyte, are not inconsistent with more highly organised plants having already existed at that period. The information on this point is insufficient, but large stems which bore regularly arranged lateral appendages and other stems with suggestively complex internal structure are known. It is the undoubted existence at that period of very simply organised vascular plants that is the fact of critical importance.

Though DAWSON's restoration of *Psilophyton* was used by LIGNIER as an example of such more primitive types of land-plants, it was impossible to overlook the lack of critical evidence for some features in the reconstruction. The earlier data, though of great interest, were indeed almost always rendered less valuable owing to uncertainty regarding essential facts. The study of the Rhynie chert has fortunately added definite knowledge of the organisation of certain simple and very completely preserved plants of at least a near geological age.

The information afforded by the study of *Asteroxylon*, the most complex of the Rhynie plants, would not by itself have added fundamentally to what was already known or inferred, although it would have rendered this much more complete and certain. In *Asteroxylon* we have a plant-body with shoots consisting of stems bearing numerous relatively small leaves. The plant thus conforms, on the whole, to the type of shoot known in *Thursophyton* (*Lycopodites*) *Milleri*, *Psilophyton princeps*, and at the present day in *Lycopodium* and the Psilotaceæ. In the absence of definite roots and the possession of a simply constructed cylindrical rhizome continued directly (with the appearance of leaves and complication of the internal structure) into the aerial shoots, *Asteroxylon* shows a simpler organisation than any Lycopod. This condition is, however, found in the existing Psilotaceæ, and it presumably held also, as was stated by DAWSON, for *Psilophyton*. While some

uncertainty must remain as to the reproductive region of *Asteroxylon*, the evidence of association is in favour of the sporangia having been borne on leafless branch-systems. In this respect also *Asteroxylon* would agree with *Psilophyton*.

The general organisation of the sporophyte in *Asteroxylon* and *Psilophyton* gives us a distinct type of plant-body which contrasts with the Fern, Equisetum, and Lycopod types, but may be more closely compared with the plant-body in the existing Psilotaceæ. The Lycopod type is distinguished from the type of *Asteroxylon* in its vegetative construction by possessing true roots; the range of diversity in the roots and root-bearing organs of the Lycopodiales must, however, be noted in this connection.

The great interest of the organisation of *Asteroxylon* and *Psilophyton*, though both these plants are in their respective ways more or less specialised, is the suggestion it affords of a synthetic type, combining external and anatomical features found in distinct groups of the Vascular Cryptogams. The morphological, and to a less extent the anatomical, characters of the Psilotaceæ can be interpreted in the light of what we know of *Asteroxylon* and *Psilophyton*. The external morphology of the shoot, and especially the anatomy of *Lycopodium*, find parallels in *Asteroxylon*. The comparison between the characters of *Asteroxylon* and those found in plants of the Fern type is less apparent, but comes out especially when the Zygopteridæ are taken into consideration. The geological age of *Asteroxylon* and *Psilophyton* adds importance to the synthetic type they exhibit. The definition of the various types of Pteridophyta, that might be regarded as possibly derived from such a synthetic type, is afforded partly by vegetative form and structure, but largely by the relative positions occupied by the sporangia. The diversity attained in this respect by the Fern and Lycopod types, for example, can be most readily conceived if a branch-system bearing sporangia on some of its ultimate subdivisions is taken as the point of departure. Such a structure appears to have held for the fertile regions of the sporophytes of *Asteroxylon* and *Psilophyton*, while the vegetative shoots bore more or less crowded small leaves.

The other three plants (*Rhynia Gwynne-Vaughani*, *Rhynia major*, *Hornea Lignieri*) found at Rhynie along with *Asteroxylon* exhibit still greater simplicity of organisation in being not only rootless but leafless. They have been placed together in a very natural family called the Rhyniaceæ which, along with the Asteroxylaceæ, to which *Asteroxylon* and probably *Psilophyton* belong, represent the distinct class of the Pteridophyta which has been named the Psilophytales after its first clearly recognised member. The simple Rhyniaceæ afford a surprising addition to our knowledge of the plant-forms realised in the Vascular Cryptogams. With merely differences of detail the plant-body in *Rhynia* and *Hornea* consisted of (a) a rhizomatous, subterranean portion, bearing absorbent hairs, without leaves, and with nothing suggestive of the organisation of a root, (b) a dichotomously branched, aerial system of cylindrical axes without leaves, and (c) large sporangia

terminating some of the finer branches. This type of plant-body is simpler than anything that was previously known in plants with stomata, tracheidal vascular system, and cuticularised spores. Its demonstration is the outstanding contribution of fact which the study of the Rhynie deposit has made to the comparative morphology of the Vascular Cryptogams, and through them of the land-vegetation composed of sporophytes.

In the comparative study of the Vascular Cryptogams we must now include plants with independently living, rootless, and leafless sporophytes; these may, without exaggeration, be described as thalloid branch-systems attached to the soil by a basal region bearing rhizoids. As previously mentioned, the existence of a gametophyte or prothallus, probably of small size, can be inferred from the production of the spores in tetrads. There is nothing in these very simple sporophytes to suggest their origin by reduction from more highly organised types. Their antiquity and what we know of the peculiarities of the vegetation of the Early Devonian period add to their interest and significance.

The type of the Rhyniaceæ is so simple that a gap remains between it and even the simplest sporophytes with leafy shoots. The mode of origin of the latter type of construction, which has long been a speculative morphological problem, is thus not clearly demonstrated by the ancient leafless and leafy types that co-existed at Rhynie. This problem will be dealt with further below.

On the other hand the simplicity of organisation of the sporophyte in the Rhyniaceæ facilitates comparisons with the Bryophyta and the Algæ. While concentrating attention on the Rhynie plants as most fully known, some other Early Devonian plants must be borne in mind in such comparisons. Prominent among these plants is the incomplete and less satisfactorily preserved, stalked, columellate sporangium or sporogonium which has been named *Sporogonites* by HALLE. Another plant that must be mentioned is the peculiar *Parka*, of uncertain systematic position, in which masses of cuticularised spores have recently been shown to fill the areolæ.

As regards Bryophyta, our practical ignorance of undoubted plants of this group from any but the more recent geological formations must be remembered. It was suggested by HALLE that *Sporogonites* was the sporogonium of a Bryophyte; in the light of our knowledge of *Hornea* his alternative view that it might be the upper portion of a plant on the line of descent of the Pteridophytes appears to be more probable. All that can at present be said is that the simplicity of the independent sporophytes of the Rhyniaceæ makes comparison between the asexual generation in Bryophyta and Pteridophyta easier, and to this extent narrows the gap between these two great groups. Further than this it is not possible to go, so long as we have no knowledge of simple sporophytes permanently borne on the gametophytes; this becomes more than ever the essential distinction between Bryophyta and Pteridophyta.

The organisation of the Rhyniaceæ also facilitates comparison with Algæ. In

the case of some other Early Devonian plants, that are, however, very imperfectly known, we may with fuller knowledge have to recognise such combinations of characters as would break down any sharp distinction between the Algæ and the simplest Pteridophytes. This does not, however, appear to us to be the case for the Rhyniaceæ, and still less for the more complex Asteroxylaceæ. The combination of characters which the Rhynie plants possess (independent sporophytes, epidermis with cuticle and stomata, vascular system with characteristic tracheides, thick-walled sporangia with cuticularised spores) justify our recognising them as Vascular Cryptogams or Pteridophyta. The differences between them and other Pteridophyta are those of degree only, and are sufficiently expressed by placing them in a distinct class (Psilophytales) of this group. It can, however, be said that the members of this class are the Pteridophyta, which are most readily comparable with the Algæ; this holds most strongly at present for *Hornea*, in which stomata have not been demonstrated.

Terms implying actual relationship by descent have been deliberately avoided in the comparisons which have been made above between the plants described in this series of papers and Algæ, Bryophyta, and other Pteridophyta. The suggested comparisons are based on the observed facts of form and structure. In expressing the comparisons in terms of possible phyletic relationship we enter into a more speculative region. The characters in question are not such as to establish beyond question the course of evolution either as regards the divergent origin of the more specialised Pteridophyta from a common source, or, on the other hand, the direct derivation of the simplest Pteridophyta from any particular Algal group.

It has been pointed out in the discussion in an earlier part of this series of papers (Part III, p. 673) that the characters of *Asteroxylon* and *Psilophyton*, as representing a synthetic type, are consistent with such a divergence of the great classes of Pteridophyta from a common type as had been suggested by a number of investigators. The Psilotaceæ would be of all existing plants the least altered from this; the Lycopodiales, while specialised in various directions, would have preserved many features found in the archaic type; the Fern type, if the large leaves are regarded as specialised branch-systems, would have been more profoundly modified. It is perhaps better to regard the point of divergence as represented by plants somewhat simpler than the Asteroxylaceæ in that they did not possess definite small leaves; this assumption is rendered a natural and legitimate one by the fact that in the Rhyniaceæ we have Vascular Cryptogams which actually exhibit this simplicity.

The Rhyniaceæ lend themselves naturally, on the other hand, to comparison with Algæ, as regards external form, the absence of definite roots, and especially in their large sporangia having arisen more or less evidently by the transformation of the tips of certain branches of the thalloid plant-body. These general resemblances, as was pointed out (Part II, p. 622), "are consistent with the Rhyniaceæ finding their

place near the beginning of a current of change from an Alga-like type of plant to the type of the simpler Vascular Cryptogams."

It appears to us unwise to go further than this at present in view of the absence of evidence justifying a connection of these Vascular Cryptogams with particular Algal forms. We may anticipate sure, if slow, progress in our knowledge on this question to come from the fuller study of other plant-remains of this early geological period; caution rather than boldness is therefore advisable in speculating on the subject.

The facts described in these studies of the Rhynie plants, together with other recent work on the Early Devonian flora, do not solve the question of the mode of origin of the simplest Vascular Cryptogams. It is, therefore, only necessary to touch briefly on their bearing upon various hypotheses which have been advanced regarding this. It has been pointed out (Part II, p. 623) that the morphology of the Rhyniaceæ (while not inconsistent with the hypothesis that regards the sporophyte as an interpolated phase in the life-history) supports the views which hold the sporophyte of the Pteridophyta to have been derived by the modification of a plant-body such as is seen in the asexual stage of a number of the higher Algæ. The former views have been especially worked out by CELAKOVSKY and BOWER, while the conception of an origin of the Pteridophyta by transformation of advanced Algal forms underlies the views of POTONIÉ, LIGNIER, SCHENCK, CHURCH, and others. It is not necessary to enter here into the details of the various theories, which require to be considered in the light of the state of our knowledge at the times when they were respectively advanced.

When the attempt is made to relate in detail any of the particular hypotheses to the features of the simple Pteridophyta recently discovered it becomes evident how difficult it is to frame such speculations without assuming too much. The further knowledge of the course of the life-history in such Algæ as *Laminaria*, *Cutleria*, *Dictyota*, and the Red Sea-weeds has revealed the existence of a definite alternation of generations, with all proportional sizes of the two generations, within the Algæ. There is thus no reason, as in the earlier statements of the antithetic theory, to start with the post-sexual complications in such Green Algæ as *Coleochete*. On the other hand the absence of leaves and of any specialised root-like branches in the Rhyniaceæ gives us within the Vascular Cryptogams a simpler starting-point for the organisation of the sporophyte than is postulated by either LIGNIER or CHURCH, whose conceptions on the origin of the plant in the Vascular Cryptogams by the transformation of an Algal plant-body are the most explicitly formulated. The possibility of the type of plant in the Rhyniaceæ having been reached by an evolution on land, parallel to that of the marine algæ, is not to be dismissed as out of the question. In this connection some of the conceptions associated with the antithetic theory may possibly be found to hold.

The facts so far known seem to favour the idea of the origin of the land

sporophyte by transformation of an Algal plant-body, but are equally consistent with such ancestral Algæ having possessed an antithetic alternation of generations. They do not, however, support the detailed suggestions as to methods of advance made by either of the opposed theories, *e.g.* on the one hand the relegation of the differentiation of stem, leaves, and roots to the Algal ancestry, and on the other intercalation of the sporophyte by progressive sterilisation. If such detailed assumptions as these are put aside there is no longer the antagonism between the antithetic and homologous origin of a sporophyte that at one time seemed to hold. The simple sporophyte of *Rhynia* or *Hornea* was part of an antithetic life-history, while its organisation can be properly treated as homologous with the plant-body as realised in both the sexual and spore-bearing stages of many Algæ.

The important change in the working position of comparative morphology that has come about with the advance of our knowledge, both of Algæ and of extinct Vascular Cryptogams, is that a common consideration of the differentiation of the plant-body in Pteridophyta, Bryophyta, and Algæ is permissible and desirable. We may leave questions of phylogeny on one side, with the recognition that the characters of the Psilophytales are such as on the one hand to bring these three groups of plants closer together, and on the other to enable us to form a clearer conception of a divergence towards the other classes of Pteridophyta and the land-plants generally.

While the exact methods of advance, whether these implied actual genetic relationship or were parallel developments, must remain open questions, progress may be possible with such an extended comparative morphology. The bearing of the plants under consideration on some problems of general comparative morphology may, therefore, be referred to in conclusion. These remarks, which must necessarily be brief, may be divided into those on the origin of roots and the morphology of the protocorm, the origin of the leafy shoot and the relation between large-leaved and small-leaved types of this, the vascular system, and the nature and original position of the sporangia of Pteridophytes.

(a) *The Origin of Roots; Morphology of the Protocorm.*

The absence of definite and characteristic roots is a common feature of all the Rhynie plants; as a presumably primitive condition this is only retained by the Psilotaceæ among existing Vascular Cryptogams. In *Asteroxylon*, as in the Psilotaceæ, the extensive rhizome system suggests the possibility of the derivation of roots by its further modification, and the occurrence of exogenous roots in some Lycopodiales further narrows the gap.

The subterranean region in the Rhyniaceæ was less extensive than in *Asteroxylon* even when, as in *Rhynia*, it consisted of cylindrical branched axes resembling the stems in general structure, but bearing rhizoids. It was especially interesting in the case of *Hornea* on account of its tuberous lobed nature, the lobes being often rather

distinct, but in other specimens more or less confluent. A single, branched aerial axis sprang from each lobe. The features of this type of rhizome, though on a larger scale, have so much in common with the protocorm of the young embryonic plants of some species of *Lycopodium* that in the description it has been spoken of as the protocormous type of rhizome.

This resemblance is of great interest on account of TREUB's view that the protocorm of *Lycopodium* was the persistent relic of an organ, by which the sporophyte became physiologically related to the soil before roots had evolved. This comparison has been briefly but sufficiently treated of in Part II (p. 620). It is only necessary to repeat that the underground parts of *Hornea* appear to be consistent with and to support TREUB's view. Just as in some species of *Lycopodium* a single leaf or protophyll springs from each lobular portion of the protocorm, so in *Hornea* a single aerial branch system occupies the corresponding position. This comparison would involve a correspondence of the protophylls or leaves of *Lycopodium* with the thalloid axes of *Hornea*.

The rhizome of *Rhynia*, and the more extensive rhizome-systems in *Asteroxylon* and the existing Psilotaceæ, would then correspond morphologically to specialised extensions of the protocorm. This, as *Hornea* shows, would have been the basal region of the originally thalloid plant-body.

On the other hand the subterranean rhizome-system of these rootless plants may be compared with the attaching region of certain Algæ. The comparison is closer with those Algæ in which a rhizome-system ramifies in sandy soil and gives off erect assimilating branch systems, than with the hold-fasts that attach many Algæ to a rocky substratum.\*

TREUB's view of the protocorm involved the idea that the embryo of the early Pteridophyta was dependent on the prothallus and required to become physiologically independent. This is so in the ontogeny and may, as he assumed, have occurred in the phylogeny, though this is not a necessary assumption. There is nothing inconsistent with this in the morphology of *Hornea*. The repetition of the protocorm, though primarily an embryonic organ, in individuals isolated in vegetative reproduction is met with in *Lycopodium*.† If this view of the original nature of the protocorm and protocormous rhizome is entertained it should be noted that it affects, though it does not destroy, the comparison with the attaching bases of thalloid Algæ. These various comparisons cannot be unravelled so long as we are completely ignorant of the history of the association between gametophyte and sporophyte in the ancestors of the Pteridophyta.

From the simplicity of the rhizome-system in the Rhyniaceæ it would seem that we are justified in assuming the appearance of specialised roots to have taken place

\* Since we are dealing with general comparative morphology, and not with relationship, another more distant comparison may be made with the leafless rhizome-system of the gametophyte of some Liverworts (e.g. Calobryaceæ).

† The repetition of the specialised tuberous protocorm of *Phylloglossum* may also be compared here.

within the evolution of the vascular land-sporophyte and are not obliged to account for them by the transformation of organs already present in complex ancestral Algæ. We may, however, as above, trace comparisons with the corresponding region of the Algal plant-body.

(b) *Nature of the Leafy Shoot; Large-Leaved and Small-Leaved Shoots.*

The simplicity of organisation of the Rhyniaceæ establishes the fact that there were early Vascular Cryptogams in which the aerial parts consisted of a thalloid branch-system. This is in favour of the view that the differentiation of a shoot, with axis and leaves (though attained in the higher members of several groups of Algæ) was independently elaborated in the early land-plants. It is of course possible that in some cases a more completely differentiated land-plant might have been directly derived from an Algal form with stem and leaves, but the existence of these simpler vascular plants renders it unnecessary to assume this without evidence. They bring the origin of the distinction of stem and leaf in a shoot within the evolution of the land sporophyte, although a corresponding differentiation is attained in various Algæ and in the gametophyte of Bryophyta. Without entering into a full consideration of the problems of the relation of stem and leaf in the shoot, we have to note the comparisons which may be made with the Rhynie plants and how these bear on this much-discussed problem.

In the first place it may be noted again how closely the thalloid plant-body of the leafless Rhyniaceæ can be compared with that of many Algæ. The comparative problem of the origin of shoots with small or large leaves subordinated to a stem thus presents itself in both the Algæ and the Vascular plants. Further insight as regards either group will bear on the problem in the other, quite apart from genetic relationship.

The question of the comparison of a shoot in which the stem is clothed with small leaves with the leafless thalloid axis may be taken first, since it is presented to us directly by the co-existence of *Asteroxylon* with the Rhyniaceæ. In *Asteroxylon* a gradual passage from the leafless rhizome into the shoot and the appearance at first of small scale-leaves without vascular bundles can be followed; this is essentially similar to what is seen in *Psilotum* and *Tmesipteris*. The insertion, and in the case of the living forms the development, of these leaves appear lateral. Certain features of the shoots of the Psilotaceæ, especially of *Tmesipteris*, indicate, however, that this is not inconsistent with an interpretation of such small leaves on the lines of their being specialised branches subordinated to, and overtopped by, the further growth of the shoot. There is no clear evidence of this, however, and all that can be said in its favour at present is that the dichotomous branch system of the Rhyniaceæ provides us with the sort of starting-point from which small leaf-like branches originate in this way in certain Algæ.

Between the leafy shoots of *Asteroxylon* and the leafless, dichotomous thalloid

plant-body of the Rhyniaceæ there is, as has already been pointed out, a distinct gap. We have kept our minds open to the possibility that the hemispherical projections on many stems of *Rhynia Gwynne-Vaughani* might be regarded as indicating a step towards the origin of small and truly lateral leaves; this was indicated as one of two alternatives in Part III (p. 674). There were always difficulties in such an interpretation apparent to us. The late origin of these hemispherical projections underneath the stomata that we have now been able to demonstrate (pp. 832-834) seems to further weigh against entertaining it, although the specimen represented in fig. 10 lends it some support. The only possible conclusion at present appears to be that the Rhyniaceæ afford no clear indication as to the first origin of leaves.

Another question raised by speculative morphology on which the bearing of the Rhynic plants must be considered is as to whether a distinction should be drawn between the small leaves (e.g. of *Lycopodium*) and the large leaf or frond of such plants as the Ferns. The clearest statement of such a view is that by LIGNIER, who derived it partly from a consideration of the reconstruction of *Psilophyton*. He distinguished the small leaves of Lycopods as phylloids from the specialised branch-systems or cauloids which gave rise to the fern-frond.

On this question also the morphology of the Rhynic plants does not afford direct evidence—though, as has been pointed out in Part III, it is not inconsistent with such an interpretation. The most significant fact provided by the newly discovered plants is the demonstration in the Rhyniaceæ of Vascular Cryptogams with a thalloid plant-body without small leaves or phylloids. It is, therefore, not necessary to assume that such phylloids have been lost from the branch-systems forming fern-fronds, though this possibility is open to evidence as to whether in particular examples it was or was not the case.

On the further question of whether a distinction is to be drawn between the origin of relatively small leaves and of larger subordinated branch-systems the Rhynic plants also do not give any clear evidence. On the whole their organisation seems to weigh against drawing too sharp a distinction and to support TANSLEY'S modification of LIGNIER'S view.

It should be borne in mind that there is evidence in the Early Devonian period of stems bearing definitely arranged, large, lateral appendages that can clearly be regarded as specialised subordinated branch-systems or fronds. With fuller knowledge of such plants more definite evidence on the comparative problems indicated above may be anticipated.

### (c) *The Vascular System.*

All the Rhynic plants had a well-developed, though simple, vascular system with characteristically thickened tracheides forming the xylem, which was surrounded by a tissue differing from the parenchymatous ground tissue and corresponding to the phloem.

The structure of even the more simple Rhyniaceæ in this respect differs markedly from what has been observed in any known Algæ, and no pertinent comparisons can be made with these plants. It is also unnecessary to do more than mention without entering into detailed comparisons the simple strands of narrow lignified cells found in the midrib of the thallus in a few genera of Hepaticæ.

In the Rhyniaceæ the structure of the simple vascular strand or stele is similar throughout the plant. A feature of interest is the distinction of central and peripheral xylem seen in the steles of *Rhynia major* and *Hornea* and in the stouter strands of xylem of *Rhynia Gwynne-Vaughani*. Though the central xylem of these plants is not clearly protoxylem, it is perhaps justifiable to compare the arrangement with the centrarch construction of the leaf-traces of *Asteroxylon* and many species of *Lycopodium* and the stem-steles of some existing and extinct Vascular Cryptogams.

The complicated vascular system of the stem of *Asteroxylon* is not easy to adequately compare with the simple vascular structure of the Rhyniaceæ. This difficulty is intimately connected with the gap between the leafless condition of the latter and the leafy condition of the stem of the former plant which has been emphasised in the preceding section. Another difficulty that may be pointed out is that those regions of *Asteroxylon* in which the vascular strand is simplest (rhizome, branch-traces) have a solid strand of xylem with no indication of protoxylem. Protoxylem is clearly present in the leaf-traces and appears in the arms of the stellate xylem of the stem-stele. The attempt to interpret the complex xylem of the leafy stem of *Asteroxylon* at once introduces the problem of the respective parts played in its construction by a cauline strand and by decurrent leaf-traces. However this may be, the resulting stele is remarkably comparable with the stele of *Lycopodium*, although the type of thickening of its tracheides is quite peculiar to *Asteroxylon*. The resemblance to the stellate stem-steles of some Zygopteridæ, though not so close, must also be mentioned. It may be pointed out that there is also a possible comparison between the leaf-trace "receptors" and the central mass of metaxylem of the *Asteroxylon* stele and the receptors and the apolar connecting bar in the petiolar bundles of the Zygopteridæ. These comparisons are the more significant in the light of the various points of resemblance between *Asteroxylon* and both *Stavropteris* and *Lycopodium*.

Such general questions concerning stelar anatomy are too wide to be entered upon here, and may be left with these brief comparative remarks.

(d) *Position and Nature of the Sporangia of Pteridophyta.*

The Rhynie plants appear to afford some definite information on the nature and original position of the sporangia in the Pteridophyta. In the absence of evidence of actual origin in descent of one great group of plants from another, we can only recognise the way in which the sporangia of *Rhynia* and *Hornea*

facilitate comparison on the one hand with the spore-bearing organs of the more specialised Pteridophyta, and on the other hand with Bryophyta and especially with Algæ.

As regards the position of the sporangia, it is clear that in *Rhynia* and *Hornea* they occupied the ends of some branches of the thalloid plant-body. There is strong reason to hold that the position of the sporangia on certain branch-systems of the more complex plant of *Asteroxylon* and *Psilophyton* was similar. If, as appears to be the case, we are here dealing with generalised early plants representing the precursors of the more specialised groups of Pteridophyta, it is reasonable to expect that the position of the sporangia in the Psilophytales should be consistent with and explain the diverse specialised positions they occupy in later derived groups. This is as a matter of fact the case; the position of the sporangia of the Rhyniaceæ at the tips of thalloid branches appears to fit naturally with conclusions arrived at from other points of view by a number of investigators of the Pteridophyta.

Thus this conception applies readily to sporangiophores bearing one or more sporangia such as are met with in what have been termed the sporangiophoric Pteridophyta and in some others. The sporangiophores would appear to represent the last persisting remains of the original leafless branch-systems of the Rhyniaceæ. It is unnecessary to follow this comparison into detail, but it may be pointed out that it applies to such cases as the sporangiophores of *Helminthostachys*, of the Equisetales and Sphenophyllales, in a somewhat different fashion to the fertile appendages of the Psilotaceæ, and with greater difficulty and obscurity to the position of the sporangia of the Lycopodiales.

In the case of the Ferns there is no difficulty in the comparison of the terminal position of sporangia on the ultimate ramifications of a branch-system with the marginal position on a webbed cladode-system of pinnules forming a definite flattened frond. This was suggested in detail by LIGNIER (taking *Psilophyton* as a starting-point), and he further followed the change in position of sporangia to the lower surface of the frond. BOWER's more recent conclusions envisage the marginal position of the sporangia as the probable starting-point in the case of Ferns and support these comparisons from the side of the spore-producing organs of the higher Ferns.

As regards the structure of the sporangia themselves, there are two very distinct types or grades in the Rhynie plants. The fairly large sporangia referred to *Asteroxylon* (which are, however, relatively small compared with those of the Rhyniaceæ) had a definite dehiscence depending on the structure of the sporangial wall. They are thus comparable with the specialised sporangia found in most existing and extinct Pteridophyta, and are very similar to those of *Stauropteris*. The sporangia of *Rhynia* and *Hornea*, on the other hand, which in *Rhynia major* were of relatively huge size, show no arrangements for dehiscence although the epidermal layer of cells is specially thickened.

A very important and striking feature of the sporangia of *Rhynia* and *Hornea* is the indication they afford of the sporangium being the transformed and specialised tip of a branch of the thalloid plant-body. This was shown especially in some less-defined specimens of the sporangia of *Rhynia Gwynne-Vaughani*, which appeared to have a group of spore-tetrads developed within a structure like the tip of a vegetative branch (Part II, figs. 10, 11). It is also shown in the way\* in which the dichotomy of the tip of a branch in *Hornea* affects the sporangia developed from it; we meet with both simple and branched sporangia. While from one point of view and as regards some specimens the sporangia of the Rhyniaceæ can be regarded as specialised organs contrasting with the vegetative axes, from another point of view they are clearly seen to be the modified tips of the latter.

These considerations are significant when the sporangia of the Rhyniaceæ are compared with the corresponding structures in the Bryophyta and the Algæ.

As regards the Bryophyta, it is only possible to recognise that the types of sporangia in *Rhynia* and *Hornea* facilitate comparison with certain sporogonia. This applies to the enclosed position in which the spores are produced, protected by a more or less massive wall, and to the presence in some cases of a sterile columella, so that the spores lie between this and the wall. In the absence of any indication as to whether the sporophytic generation in Bryophyta is to be regarded as reduced, or as illustrating an independent line of progression, it seems inadvisable to pursue the comparison in greater detail. The comparisons to be made with the Algæ may, however, apply to the Bryophyta as well as to the Rhyniaceæ on which they are based.

When the comparison is extended to the Algæ it evidently bears on the primitive nature and origin of the structures which in the Rhyniaceæ and throughout the Pteridophyta are known as sporangia. These have for long been regarded as organs *sui generis* and not explained on the grounds of possible derivation with modification from any part of the plant-body of the Algæ. It has, however, been pointed out by SCHENCK\* that, when the comparison is extended to what we term sporangia in various Algæ, the strictly comparable structures are the spore-mother-cell and resulting tetrad in the Vascular Cryptogams and the sporangia (tetra-sporangia, etc.) in which reduction and spore-formation takes place in the Algæ. SCHENCK therefore suggested employing the name "sporotheca" for the organ usually known as the sporangium in Pteridophyta. On this view the sporangium (or sporotheca) of the Vascular Cryptogams (and the sporogonium of Bryophyta) would correspond to an association of a large number of sporangia of the thallophyte type enclosed within a special region of the plant-body.

The type of sporangium (sporotheca) in *Rhynia* and *Hornea* appears to strengthen and support the view based on the above comparison. It has been pointed out in Part II (p. 622) how their construction suggests comparison with the

\* Engler's *Bot. Jahrb.*, Bd. xlii (1908), p. 31.

specialised branches of some Red Sea-weeds, in which the numerous tetrasporangia are enclosed by a wall-like outer layer of the branch and may surround a central axis that would correspond to the columella. The specialised tetraspore-bearing branches are called stichidia. They not only occur as terminal organs of the thallus, but may stand in definite relation to laterally placed vegetative branches.

Advancing knowledge of the spore-producing structures in the Early Devonian plants may be expected to throw further light on such comparisons, which it is not advisable to press too far at present. The facts appear, however, to fully warrant the suggestion that the structure known as the sporangium in the Vascular Cryptogams may be regarded as corresponding to the tip of a branch of a thalloid sporophyte enclosing the sunken tetrasporangia represented by the spore-mother-cells. On this view the sporangium of the Pteridophyta would not be an organ *sui generis*, although in considering its further modifications in the Pteridophyta it may be treated as if it were a primary member of the plant.

In this section we have placed together our conclusions as to the main bearings of the new facts obtained by the study of the Vascular plants of Early Devonian age found at Rhynie on the comparative morphology of certain extinct and existing plants. While it appears inadvisable to omit such a general discussion, we would explicitly point out that we regard all such comparisons as to a certain extent tentative. They are thus distinct from the addition to our definite knowledge of the plants which it is the primary object of this series of papers to make known.

In conclusion a word may be said as to the bearing of the Vascular Cryptogams in the Rhynie peat on the geological age of the deposit. That some plants of similar morphological character exist in both the Lower and Middle Old Red Sandstone of Scotland seems to be certain, although no clearly defined species has yet been recorded as common to both. In the Middle Old Red Sandstone neither *Psilophyton* nor *Arthrostroma*, two characteristic Lower Old Red Sandstone plants, have yet been recorded on satisfactory evidence. On the other hand, no such leafy plant as *Thursophyton Milleri*, which is a most characteristic species of the Middle Old Red Sandstone, has been discovered in the Lower Old Red. If the leafy shoots of *Asteroxylon Mackiei* and those of *Thursophyton Milleri* are compared, taking the probable sizes of the plants into consideration, the similarity is very striking. The similarity is indeed so great as to suggest that they may be only different conditions of preservation of one species. It seems at present desirable, however, to treat them as distinct in the hope of additional light being thrown on their relation to each other. In any case it is clear that *Asteroxylon Mackiei* in its leafy shoots exhibits a close similarity to *Thursophyton Milleri*, and, even if not specifically identifiable with it, represents a characteristic type of plant which so far as at present known is absent from the Lower Old Red Sandstone. These facts taken together lead us to believe with but little reservation that the Rhynie chert-band is almost certainly of Middle Old Red Sandstone age.

## EXPLANATION OF PLATES.

(We are indebted to Mr J. BARRIE ROBINSON for re-drawing our reconstructions of the vascular plants reproduced on Plates I and II. All the figures on Plates III, IV, and V are from untouched photographs.)

## PLATE I.

Fig. 1. Restoration of *Rhynia Gwynne-Vaughani*.

Fig. 2. Restoration of *Rhynia major*.

## PLATE II.

Fig. 3. Restoration of *Hornea Lignieri*.

Fig. 4. Restoration of *Asterozylon Mackiei*.

## PLATE III.

Fig. 5. Vertical section of a typical hemispherical projection from a longitudinal section of a stem of *Rhynia Gwynne-Vaughani*.  $\times 100$ . (No. 2514.)

Fig. 6. Tangential section of stem of *Rhynia Gwynne-Vaughani* bearing two hemispherical projections, while another has been isolated by the section from the same stem and is seen on the extreme right.  $\times 30$ . (No. 2514.)

Fig. 7. Portion of specimen in fig. 6 showing the position of the stomata in relation to the two attached projections. s., stoma.  $\times 60$ . (No. 2514.)

Fig. 8. The detached projection in fig. 6 showing the stoma (s.) with its two guard-cells.  $\times 60$ . (No. 2514.)

Fig. 9. Small hemispherical projection forming beneath a stoma (s.). From a tangential section of the stem of *Rhynia Gwynne-Vaughani*.  $\times 200$ . (No. 2423.)

Fig. 10. Hemispherical projection on a stem of *Rhynia Gwynne-Vaughani*, elongated to form a cylindrical emergence.  $\times 24$ . (No. 2515.)

Fig. 11. Longitudinal section of a stem of *Rhynia Gwynne-Vaughani* showing a hemispherical projection on the right, and on the left two necrosed areas.  $\times 14$ . (No. 2516.)

Fig. 12. Necrosis cavity from a longitudinal section of the stem of *Rhynia Gwynne-Vaughani*. The cavity is still roofed over by the cuticle and is bounded by cells that have undergone enlargement and cell-division.  $\times 50$ . (No. 2414.)

Fig. 13. Transverse section of stem of *Rhynia Gwynne-Vaughani* showing a necrosis cavity and the enlargement and division of the cells around this.  $\times 38$ . (No. 2406.)

Fig. 14. Oblique section of stem of *Rhynia Gwynne-Vaughani* showing a large necrosis cavity, the cells around which are proliferating.  $\times 36$ . (No. 2517.)

## PLATE IV.

Fig. 15. Portion of fig. 14 more highly magnified, showing the proliferating cells in the neighbourhood of the xylem.  $\times 100$ . (No. 2517.)

Fig. 16. Stem of *Rhynia Gwynne-Vaughani* with vertically elongated and dividing cells bordering on a necrosed area.  $\times 50$ . (No. 2427.)

Fig. 17. Longitudinal section of tip of stem of *Rhynia major*.  $\times 28$ . (No. 2518.)

Fig. 18. Apex from fig. 17 more highly magnified showing the gradual enlargement of cells behind the apical meristem.  $\times 65$ . (No. 2518.)

Fig. 19. Two stems of *Rhynia major* in transverse section. The stem on the right shows a dark necrosed area and in relation to this callus-like disturbance and proliferation of the tissues. The stem on the left shows a large cavity and similar pathological changes in the tissues.  $\times 15$ . (No. 2519.)

Fig. 20. Portion of the wound-tissue from the stem on the left in Fig. 19.  $\times 100$ . (No. 2519.)

Fig. 21. Portion of the wound-tissue from the stem on the right in Fig. 19.  $\times 100$ . (No. 2519.)

Fig. 22. Stem of *Rhynia Gwynne-Vaughani* in transverse section showing enlargement of the cells in certain regions as compared with others where the cells are of normal size.  $\times 22$ . (No. 2520.)

Fig. 23. *Asteroxylon Mackiei*. Portion of cuticle of a stem viewed obliquely from the surface. The longitudinal dark lines on the epidermal cells are shown.  $\times 100$ . (No. 2479.)

PLATE V.

*Asteroxylon Mackiei*.

Fig. 24. Section of the chert showing a large rhizome bending downwards into the peat and penetrating a large stem in the latter; the basal region of the rhizome bears small scale-leaves.  $\times 3\frac{1}{2}$ . (No. 2557.)

Fig. 25. Transverse section of the bud of a leafy shoot, passing just above the apical cone and showing the arrangement of the small leaves.  $\times 14$ . (No. 2554.)

Fig. 26. Transverse section of the stem from the same series as the preceding figure passing immediately below the apex.  $\times 14$ . (No. 2553.)

Fig. 27. Portion of the section in fig. 26 more highly magnified. *ep.*, epidermis; *o.c.*, outer cortex; *i.c.o.*, outer zone of inner cortex; *i.c.m.*, trabecular middle zone of inner cortex; *i.c.i.*, inner zone of inner cortex; *l.t.*, departing leaf-traces; *x.*, xylem of the ends of the rays of the stellate xylem.  $\times 35$ . (No. 2553.)

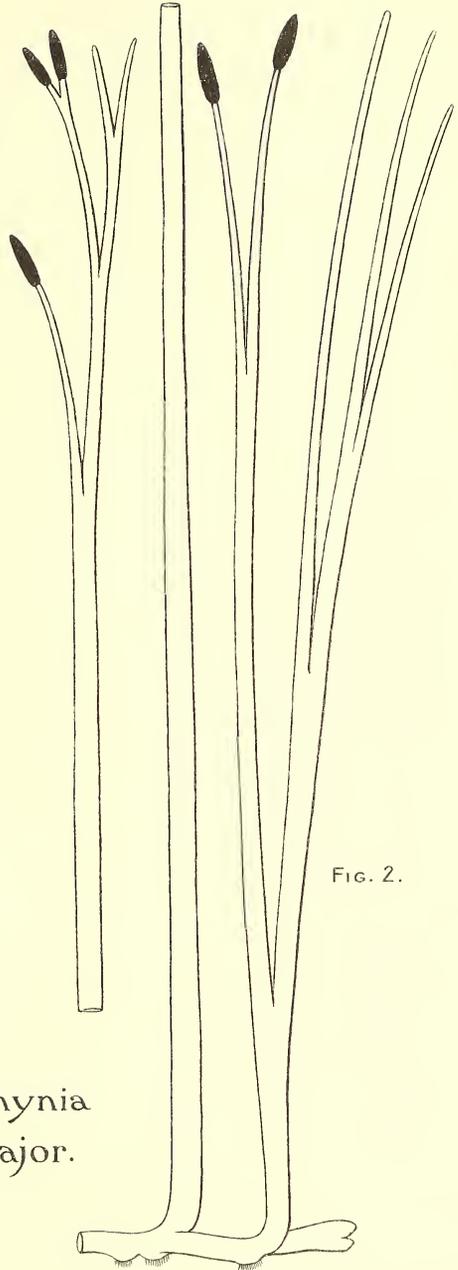
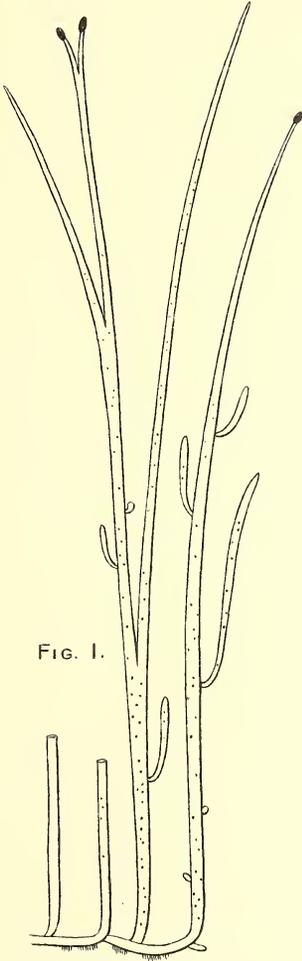
Fig. 28. Stele of a section lower in the series showing the poles of the stellate xylem still unconnected by central xylem.  $\times 50$ . (No. 2550.)

Fig. 29. Transverse section of the stem at the lowest level in the series.  $\times 14$ . (No. 2547.)

Fig. 30. The stele of the section shown in Fig. 29. The central xylem is still undifferentiated except for a few tracheides.  $\times 50$ . (No. 2547.)

We again gratefully acknowledge our indebtedness to the Executive Committee of the Carnegie Trust for a grant to defray the expense of the plates illustrating this memoir.

Rhynia  
Guynne-Vaughani.





Asteroxylon  
Mackiei

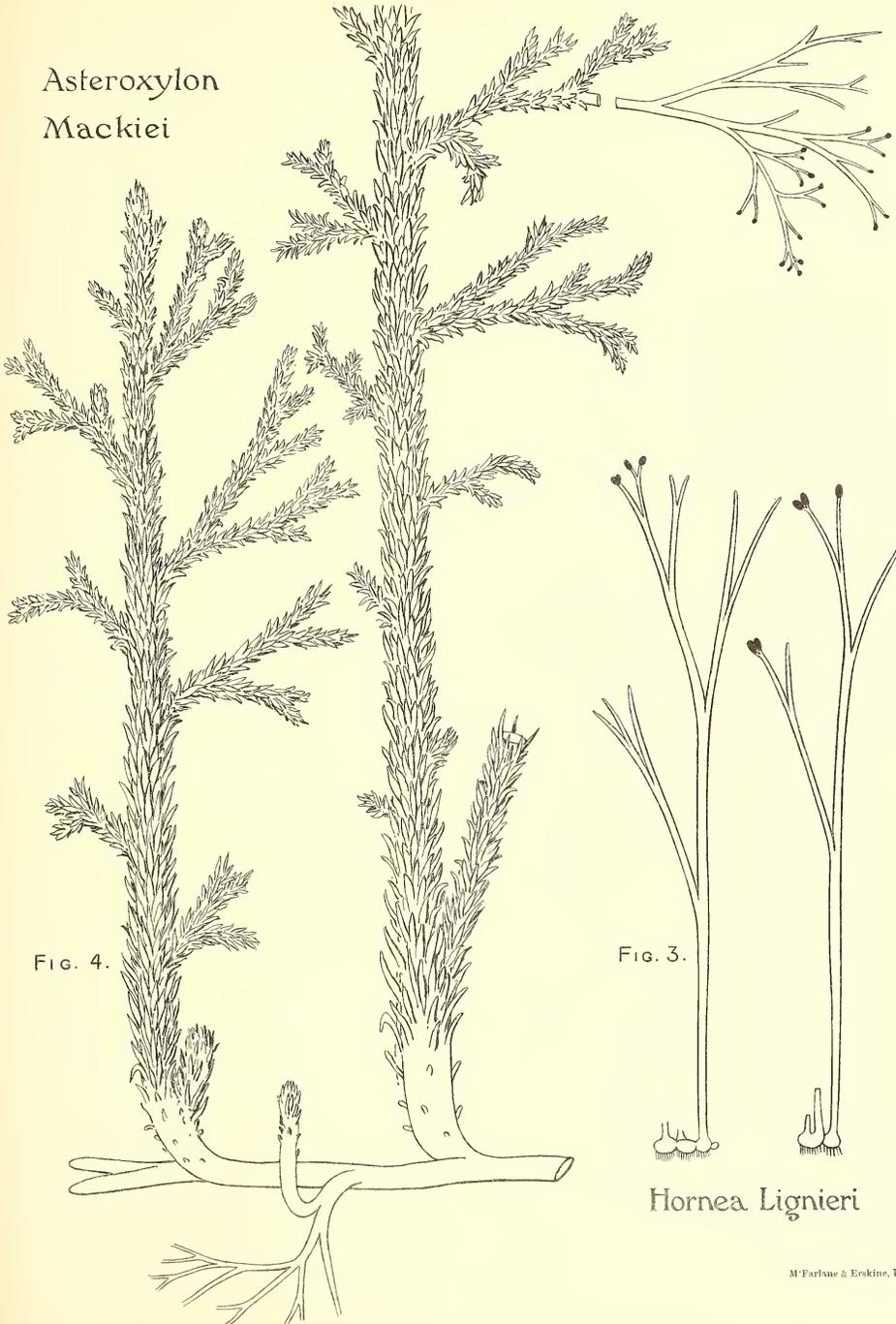


FIG. 4.

FIG. 3.

*Hornea Lignieri*





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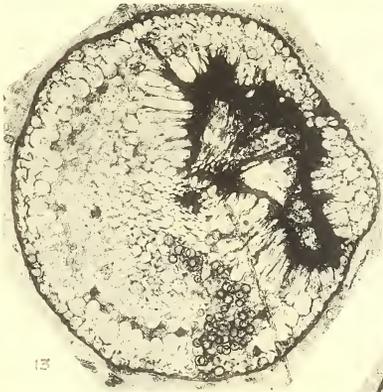
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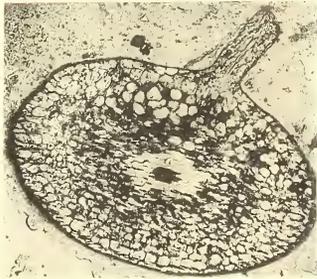
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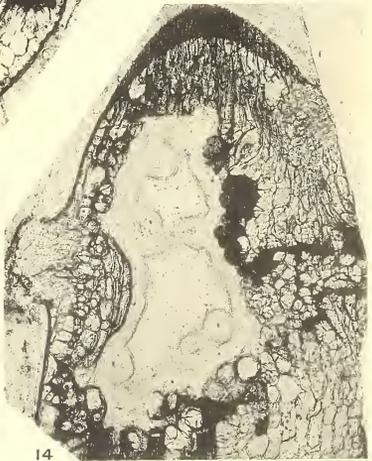
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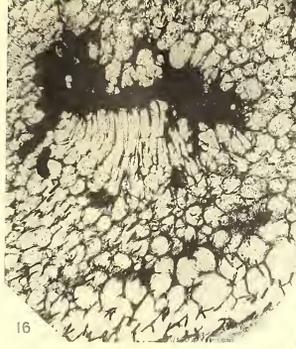


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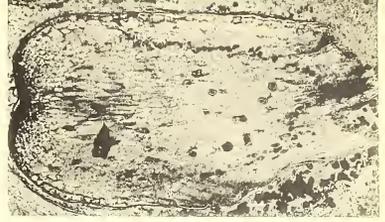




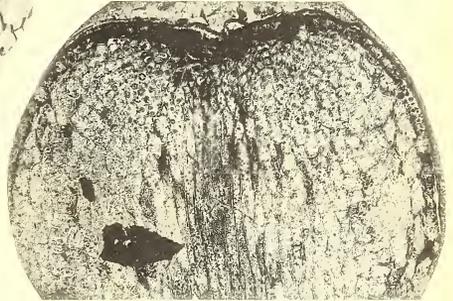
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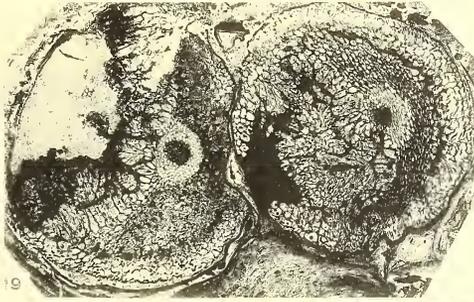
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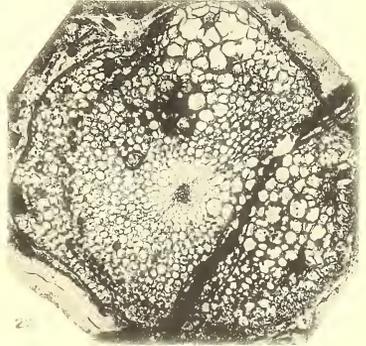
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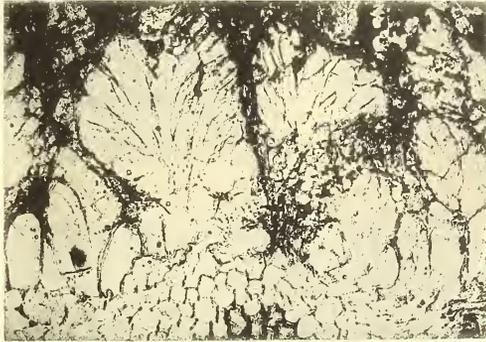
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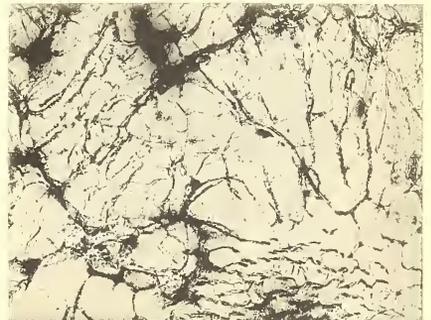
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KIDSTON AND LANG. PHOTO.

FIGS. 15, 16 — RHYNIA GWYNNE-VAUCHANI, K&L.

FIGS. 17-22 RHYNIA MAJOR, K&L.

FIG. 23. ASTEROXYLON MACKIEI, K&L.

ZINCO COLLOTYPE CO., EDINBURGH.



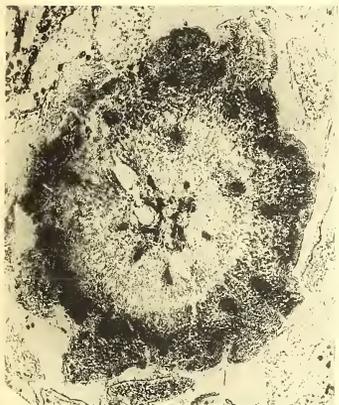
KIDSTON AND LANG. - PLATE V



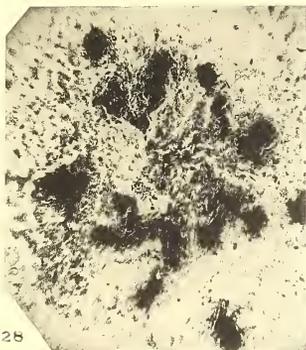
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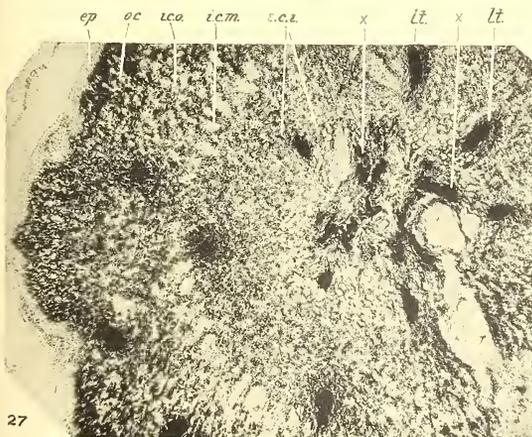
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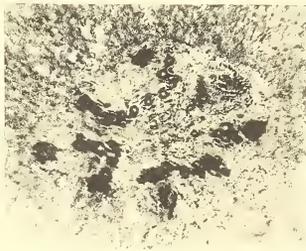
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XXXIII.—On Old Red Sandstone Plants showing Structure, from the Rhynie Chert Bed, Aberdeenshire. Part V. The Thallophyta occurring in the Peat-Bed; the Succession of the Plants throughout a Vertical Section of the Bed, and the Conditions of Accumulation and Preservation of the Deposit. By R. Kidston, LL.D., D.Sc., F.R.S., and W. H. Lang, D.Sc., F.R.S., Barker Professor of Cryptogamic Botany in the University of Manchester. (With Ten Plates and One Figure in the Text.)

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In this concluding part of the series of papers\* on the plants preserved in the Rhynie chert-band, various remains of lower plants that occur in the peat will be described, and some general questions concerning the accumulation and preservation of the deposit considered. The paper is divided naturally into the parts enumerated below.

1. An account will be given of a number of forms of Fungi which are met with in the decayed remains of the vascular plants, and also in the peaty matrix. The fungal remains are so generally distributed that they can be regarded as forming an integral part of the peat. In connection with them, the question as to whether there is evidence of a mycorrhizal relation between any of the Fungi and the Vascular Cryptogams will be considered.

2. The occurrence of Schizophyta will then be considered and a few well-characterised forms, that can be placed in this group, described.

3. A remarkable algal organism, to which the name *Algites (Palæonitella) Craniæ* is given, will be described; scattered remains of this have been found at a few spots in the deposit, and we provisionally associate with these some interesting but more doubtful remains.

4. Certain fragments that belong to an organism with the characteristic structure of *Nematophyton* will be described and discussed. These have been met with in a limited region of one block of the chert.

5. The succession of the plants, as determined by the study of a vertical series of microscopic preparations, extending from the bottom to the top of a complete section collected when the Rhynie deposit was exposed *in situ*, will be described.

6. In the light of these facts and of some others obtained from loose blocks of the chert, the question of the conditions of accumulation and preservation of the Rhynie deposit will be briefly considered.

More exhaustive study of the deposit will doubtless lead to the recognition of further types of Thallophyta, and add to our knowledge of some of those described

\* Part I, *Trans. Roy. Soc. Edin.*, vol. li, p. 761; Part II, *ibid.*, vol. lii, p. 603; Part III, *ibid.*, vol. lii, p. 643; Part IV, *ibid.*, vol. lii, p. 831.

below. It is probable, however, that the forms which have been met with in the examination of the numerous sections prepared for the study of the vascular plants and the composition of the deposit afford a not inadequate idea of the remains of lower plants preserved in the Rhynie peat-bed. Their description will fittingly complete the account of our investigation of the Botany of the deposit.

#### 1. THE FUNGI OF THE RHYNIE DEPOSIT.

The most abundant remains of lower plants in the Rhynie deposit are clearly Fungi, of which a considerable number of forms can be distinguished. Along with Bacteria, which will be considered in the next section, they formed an integral constituent of the peaty mass, as they do of recent peats.

Although the fungi are often as perfectly preserved as were the vascular plants, they do not afford characters that are reliable as evidence of their classificatory position. All the fungal remains to be described below consist of stout or fine hyphæ of the vegetative mycelium and various types of vesicles and resting-spores (chlamydospores) borne on this. The mycelium is usually non-septate, although one example of a clearly septate condition will be described.

Even when they appear to retain recognisable forms that recur in the deposit, it is hardly possible to be sure of the specific distinctness of the various types of mycelium with resting-spores found in the more or less decayed plant-remains and the peaty matrix. No student of existing fungi would, we believe, feel justified in distinguishing fungi found in a mixed growth in decayed organic matter when he had only vegetative mycelium and chlamydospores to deal with. Distinctive reproductive organs or constancy under culture would be required, even in the case of Imperfect Fungi, and the investigator would be prepared for the same species assuming a variety of forms as regards diameter of hyphæ and size of resting-spores.

It is necessary, however, to bring as much order as possible into the description of the various fungi met with so abundantly in the fossil condition in the Rhynie peat. The plan adopted will be to describe and illustrate the main form-types depending on appearance, relative size, and also in part on the place of occurrence. The possibility of distinguishing specific forms will then be considered, and some well-characterised forms will be named and diagnoses given for them.

We have deliberately ignored doubtful remains, and in all cases sought for evidence of definite organisation, such as the attachment of vesicles or spores to hyphæ, or the structure of the spore-wall.

The fungi occur mainly in the portions of the vascular plants, but to some extent in the matrix. In most cases they had evidently lived as saprophytes. The question as to whether any of them may have been mycorrhizal during the life of the vascular plants will require consideration in the general discussion which will follow the particular descriptions.

*(a) Description of Form-types of Fungi recognised in the Rhynie Peat.**Fungus No. 1. (Figs. 1-4.)*

The mycelium of the various types of fungi to be described below will be seen to be, as a rule, non-septate. The specimen here described and figured agrees in the general characters of the mycelium with some other fungi to be considered later, but shows more or less numerous transverse walls in some, at least, of the hyphæ. It is further interesting in that the hyphæ are associated in strands which, as is not unusual, occupied the place of the phloem in a partially decayed stem of *Asteroxylon*; the stem was cut longitudinally, and therefore shows a strand of hyphæ on each side of the xylem (figs. 1 and 2). The stout hyphæ run on the whole parallel to one another, and are branched without any relation to the position of the septa. At places the branches form peculiar tangles or knots (fig. 2), but, though anastomoses not improbably occurred, there are no indications of clamp-connections. The transverse septa, the middle portion of which is often thicker and of a darker colour than the outer walls of the hyphæ, occur at irregular intervals. They were frequent and distinct in the strand seen on one side of the stele (fig. 1), while they were present, though less frequent, in the strand on the other side (fig. 2). Some of the septate hyphæ are shown more highly magnified in fig. 3, and some of the non-septate hyphæ in fig. 4. The same stem of *Asteroxylon* also contained the large resting-spores of the fungal type that will be next described as Fungus No. 2. The mycelium here described as No. 1 not improbably belongs to the fungus which bore the large resting-spores, though direct proof of this is wanting. Similar strands of hyphæ replacing the phloem in a stem of *Asteroxylon*, associated with the larger resting-spores of Fungus No. 2 in the cortex of the stem, are seen in the section represented in fig. 5.

*Fungus No. 2.\* (Figs. 5-11.)*

This fungal type is probably the most widely distributed throughout the chert-bed. It occurs in fragments of all the vascular plants and is associated with their greater or less decay. It is most abundant and characteristically developed in the stems of *Rhynia major* and of *Asteroxylon* (cf. Part III, figs. 31, 42, 43, 96).

In its typical form it has stout hyphæ, as well as finer branches. The hyphæ usually appear non-septate, but in relation to this the remarks under Fungus No. 1 should be borne in mind. They bear large oval, thick-walled resting-spores, the wall of which consists of a number of layers and tends to exhibit a double contour. The general appearance of the fungus as it occurs in the decayed cortex of a stem of *Asteroxylon* is well shown in fig. 6, and more highly magnified in fig. 7. In this specimen the hyphæ were clearly shown, and bore smaller thin-walled vesicles as well as the mature resting-spores; the smaller structures were evidently stages

\* Named *Palæomyces Gordonii* below (p. 868).

in the development of the latter. The description will be based on such a typical growth of the fungus, in which practically everything that a wide comparison of other specimens has shown can be seen.

The longitudinally running hyphæ in the specimen represented in figs. 6 and 7 occurred in the inner cortex of a stem of *Asteroxylon*, the cellular structure of which had practically disappeared. Though not as perfectly preserved as is often the case, the hyphæ can be clearly traced. They range in diameter from about  $6\ \mu$  (fig. 8) to 16 or  $24\ \mu$  (fig. 9). A fine hypha sometimes widens out into one of the stouter brown-walled hyphæ (fig. 9). The hyphæ, here and in other cases where they have been seen both in the cortex and occupying the place of the phloem (*cf.* fig. 5) appear non-septate.

In fig. 7 some of the hyphæ widen out into oval or pear-shaped thin-walled vesicles, collapsed specimens of which also occur. All stages intermediate between these and the mature thick-walled resting-spores are found. The oval or spherical resting-spores are of large size (about  $240\ \mu$  in major diameter, but with considerable variation\*), and usually show the double contour of the wall that is evident in figs. 6 and 7, and to which reference has already been made. In favourable cases they can be seen to be borne on a hyphal stalk, often, as in fig. 9, arising as a lateral branch from a longitudinally running hypha.

The double contour when best marked (fig. 10) is seen to depend on the presence of a clear space separating an outer boundary layer of a brown colour from an inner more or less thick layer. Within this, again, there may be remains of the contracted and more or less indistinct contents. Sometimes an intermediate layer of the wall can be distinguished in place of the clear space; in other specimens this intermediate region is occupied by a brownish material; in yet other specimens the inner layer appears to be connected with the outer layer by fine brown strands crossing the space (fig. 11). Comparison of numerous specimens supports the impression given by these facts that we have to do with the distinction of layers in an original wall and the contraction of an inner layer.

The resemblance which the spores with double contour at first sight present to an oogonium containing a single oospore is thus a superficial one. Nothing to establish or justify such an interpretation has been found, though carefully looked for.

Nothing could be ascertained with certainty regarding the contracted contents sometimes present within the inner wall, and seen in the figures. The occurrence of smaller intrusive fungi within these resting-spores will be dealt with separately below (p. 864).

*Fungus No. 3.* † (Figs. 12–14.)

It is necessary to distinguish as a separate form-type of fungus certain thick-walled spherical resting-spores borne on stout hyphæ and resembling in construction

\* Thus the specimens in fig. 5 are over  $350\ \mu$ .

† Named *Palaeomyces Gordonii* var. *major* below (p. 868).

those of the fungus described above under Fungus No. 2. These resting-spores, specimens of which are represented in figs. 12 and 13, were about twice the size of those of the preceding fungus, their diameter being about  $500 \mu$ , though the specimens in this case also exhibit considerable differences in size. The thick hyphal stalk bearing the resting-spore is all that has been seen of the mycelium of this type. Although when typically developed this is a very distinct form, it must be kept in connection with Fungus No. 2, since specimens of resting-spores intermediate in size have been met with (*cf.* fig. 12 on the right). These large resting-spores do not show the distinct double wall that is so often, though not always, met with in the preceding form. The thick wall (fig. 14) is here best described as distinctly stratified. There is first an outer layer, the surface of which is brown; then a wide, intermediate, more or less clear layer; and lastly, an inner brown layer. The intermediate layer is sometimes laminated or stratified (fig. 13). These layers remain connected, but the contents, limited by a thin or thick brown membrane, often contract more or less from the wall.

*Fungus No. 4.* (Figs. 15 and 16.)

The fungus represented in figs. 15 and 16 is placed here, since its resting-spores, like those of the two preceding forms, have thick walls showing a differentiation into layers. It occurred in a decaying portion of a stem of *Asteroxyylon*. A moderately fine mycelium was present in the tissue, and in relation to it were the thick-walled oval or spherical resting-spores shown in the figures. These are evidently mature, and, though exhibiting a rather wide range in size, the diameter of most of them is in the neighbourhood of  $120 \mu$  to  $150 \mu$ . This is considerably smaller than the spores of Fungus No. 2, from which these resting-spores also differ in the absence of any indications of separation of the layers of the wall. A few of the resting-spores in the group (which are not shown in the figure) are distinctly larger, and thus narrow the interval between this form and Fungus No. 2; on the other hand, some are distinctly smaller than the majority, and approach in this respect the resting-spores to be described next.

*Fungus No. 5.* (Figs. 17 and 18.)

This form is only placed here on account of the relatively thick wall of the small oval resting-spores, the major diameter of which was about  $60 \mu$ . It does not call for more detailed description in addition to its representation in figs. 17 and 18.

*Fungus No. 6.* (Fig. 19.)

We may place here as naturally as anywhere the rather ill-defined form of fungus shown in fig. 19. This occurred in a decaying stem of *Rhynia major*, and had the branched, non-septate mycelium, swelling into moderately small vesicles, well preserved. Since adjoining stems of *Rhynia major* showed oval thick-walled

resting-spores like Fungus No. 2, it is not improbable that we have here a similar fungus in an earlier or different condition of development. On the other hand, it presents resemblances to the following type, in which the vesicles have never been seen to pass into thick-walled resting-spores.

*Fungus No. 7.\** (Figs. 20–28.)

This fungus occurs characteristically between the cells of the inner cortex of many of the rhizomes of *Asteroxylon*, and in the axes intermediate in structure between rhizomes and stems. The region occupied is usually more or less decayed, while the fungus seems to avoid the outer cortex and phloem. The general distribution of the fungus was evident in figs. 16 and 22 of Part III.

Fig. 25 on Plate III shows the relation of the fungus to the inner and outer cortex and its general appearance. It consists of stout and fine hyphæ and vesicles. The intercellular position of the hyphæ is shown in fig. 26. Fig. 27 and fig. 20 show the hyphæ and vesicles in more decayed tissue of the inner cortex. The fungal hyphæ are non-septate, only an occasional transverse septum having been seen. The hyphæ are abundantly branched (fig. 21), and sometimes connected by anastomosing branches (fig. 22). The branches are sometimes recurved (figs. 20, 28). The ends of many of the finer branches expand as oval or spherical thin-walled vesicles which are usually not cut off by a septum from the cavity of the hypha (figs. 23 and 24). The walls of the vesicles are not specially thickened, and do not show any tendency to separate into layers or to give the appearance of a double contour.

The fact that, as a rule, when the cell walls of the tissues are preserved the fungus is intercellular has been emphasised above. Fig. 28 shows a superficial cell of the outer cortex of the rhizome in fig. 25 which has been entered by the fungus, that in this specimen was growing on the outer surface of the rhizome; a vesicle has formed on the fungus within the cell. Both the position and the behaviour of the fungus in this case are, however, exceptional.

The figures show the range in diameter of the non-septate hyphæ and also of the vesicles. This makes it impossible to state a definite characteristic size. It may be generally said that the hyphæ range in diameter from about  $4\ \mu$  to  $20\ \mu$ , while the vesicles attain a size of about  $80\ \mu$ .

*Fungus No. 8.†* (Figs. 29–35.)

This fungus is present in many of the protocorm-like rhizomes of *Hornea*, extending also into the region of the stem attached to the rhizome. It seems to be almost always present in these positions in certain beds of the peat, while it is completely absent from the same portions of *Hornea* in other beds.

The non-septate hyphæ are stout (about  $10\text{--}15\ \mu$ ) and of a dark colour (fig. 32).

\* Named *Palæomyces Asterocylis* below (p. 869).

† Named *Palæomyces Hornea* below (p. 869).

They form a characteristic reticulum as they grow between the cells of the rhizome (figs. 29, 31). Sometimes an entering hypha can be traced giving rise to this reticulum by branching (fig. 31). Felted masses or strands of hyphæ or tangled knot-like masses are present on the lower surface of some rhizomes among the bases of the rhizoids (figs. 30, 33). The entering hyphæ seem to come from this external mycelium.

In relation to the mycelium within the tissues, and sometimes outside the rhizome, there are oval dark-walled resting-spores (figs. 29, 34). In the early stage the spore has the form of a vesicle with its cavity continuous with that of the hypha. The wall of the spore, though it acquires a brown colour, does not become markedly thickened, and does not show a double contour. These spores or vesicles measure about 100  $\mu$ . Larger resting-spores of the same type, and apparently derived from these, have been met with in the adjacent peaty matrix (fig. 35).

*Fungus No. 9.\** (Figs. 36-38.)

The general distribution of this fungus, which is of common occurrence in the cortex of stems of *Asteroxyylon*, and also enters the resting-spores of Fungus No. 2, is well shown in fig. 36. The apparently non-septate hyphæ occur abundantly in the decaying tissue. The hyphæ bear spherical resting-spores with a smooth wall that is either thin or becomes slightly thickened. The wall of the resting-spore, however, frequently appears definitely thickened and rough, but critical examination shows that this appearance is due to the spore having been closely invested by a covering of the fine hyphæ. These can be traced over the original thin wall, and their tubular cavities are apparent where the invested wall is cut in section (figs. 37 and 38). The diameter of the hyphæ is about 3  $\mu$ , and of the resting-spores about 45  $\mu$ .

*Fungus No. 10.†* (Figs. 39-41.)

This form of fungus is especially common in relation to *Rhynia Gwynne-Vaughani*. It is found in the decaying stems (Part IV, fig. 13) and also in the adjoining matrix, sometimes in a sort of exudation from the hemispherical projections. Fig. 39 shows a very characteristic mass of the fungus from the peaty matrix derived from a broken-down stem, the remains of the xylem of which is seen in the upper part of the figure. This figure and the portions of the same mass more highly magnified in figs. 40 and 41 show that the fungus consists of a fine non-septate mycelium, the hyphæ of which form numerous dilatations that are sometimes intercalary, but more commonly terminal. These are cut off by septa and enlarge into the thin-walled globular resting-spores that occur scattered or more commonly in masses. What appears to be the same organism also forms longi-

\* Named *Palæomyces vestita*, below (p. 869).

† Named *Palæomyces agglomerata* below (p. 870).

tudinal rows of vesicles or spores in the cortex of stems or occupies a considerable area of the cortex.

The hyphæ are about 4 or 5  $\mu$  in thickness, and the vesicles about 40  $\mu$  in diameter.

*Fungus No. 11.* (Figs. 42 and 43.)

The fungus which we place here resembles the preceding Fungus No. 10 in miniature. It is not impossible that with further growth it may have come to resemble it more closely. It is represented in figs. 42 and 43. This fungus has been met with most commonly in decayed stems of *Rhynia Gwynne-Vaughani*, but also occurs in other plants. Most frequently it appears as relatively small masses of fine hyphæ bearing small vesicles (fig. 42). As the latter figure shows, these masses often appear as if they had been at first defined and enclosed by single cells of the tissue and had burst out from them. It sometimes occurs in the region of cells with dark contents immediately below the outer cortex of *Rhynia* (fig. 43), but may be situated much more deeply, and even close to the stele. In some cases the group of fine hyphæ of this fungus appears to have originally occupied and grown out from a resting-spore of Fungus No. 2.

*Fungus No. 12.* (Fig. 44.)

This form has much in common with that described as Fungus No. 10. It occurred, as shown in fig. 44, in somewhat decayed stems of *Rhynia Gwynne-Vaughani*, but at a slightly higher level of Bed A<sup>1</sup>. The moderately fine hyphæ enlarge into thin-walled vesicles, but the enlargement is usually a gradual one, so that the vesicles are pear-shaped rather than spherical. Their diameter measured across the widest part is rather greater than in the case of the type 10, measuring about 60  $\mu$ .

*Fungus No. 13.\** (Figs. 45-47.)

The specimen represented rather inadequately in figs 45-47, owing to the thickness and opacity of the section in which it occurred, we owe to the courtesy of Mr JOHN B. SIMPSON. The fungus was present in a decayed stem of *Rhynia Gwynne-Vaughani*. It occurred in small oval patches, and appeared as if bursting through the cuticle or epidermis of the stem; the distribution might also be explained by the patches occupying the site of thin-walled hemispherical projections that had decayed (fig. 45). The prominent structures of each patch of fungus are hyphæ radiating outwards and dilating into thin-walled vesicles. Even the larger vesicles are not divided by a septum from the hypha. The vesicles may be 100  $\mu$  in diameter, but smaller and larger specimens occur in the same patch. Fig. 46 represents one patch of fungus, while a few of the vesicles are shown more highly magnified in fig. 47.

\* Named *Palæomyces Simpsoni* below (p. 869).

*Fungus No. 14.* (Figs. 48-56.)

Fine mycelium with vesicles and resting-spores is not only met with in cells of the parenchyma of the vascular plants, but even more commonly invading, and developing within, the resting-spores of other fungal types. An example of this in the case of a fungus that also occurs distributed through the decaying tissues has already been seen in the case of Fungus No. 9, represented in fig. 36. A very definite and recurring example of this mode of occurrence in the large resting-spores of Fungus No. 3 is now to be described. Under the following type (No. 15) similar intrusive fungi within the smaller resting-spores of Fungus No. 2 will be described. The figured specimens will further afford additional examples of the resting-spores of Fungi Nos. 2 and 3.

Fungus No. 14 was repeatedly met with in the peat of the lowest bed (A<sup>n</sup>1), especially in relation to *Rhynia Gwynne-Vaughani*, and recurred among *Hornea* in the upper part of the chert-bed (Bed N 20).

Specimens such as that shown in fig. 48, which were first noticed, appeared like a distinct fungus of definite and peculiar shape. This had the form of a shortly stalked, spherical body about .5 mm. in diameter. The stalk was evidently formed of numerous fine hyphæ associated together. Similar fine hyphæ formed a peripheral layer of the spherical body and extended among the thin-walled spores composing the central mass of this. The spores were spherical or oval, and could sometimes be seen to be borne on the fine hyphæ. Some of the spores are shown more highly magnified in fig. 49.

The explanation of the definite shape of this mass of fine hyphæ bearing thin-walled spores was afforded by specimens such as those shown in figs. 50 and 51. In the specimen in fig. 50 the group of thin-walled spores is seen to occupy the cavity of a large resting-spore with the characteristic thick wall of Fungus No. 3. In this case the intrusive fungus completely filled the cavity of the large resting-spore. The spores of the intrusive fungus were less numerous and more loosely arranged in the otherwise corresponding specimen in figs. 55 and 56.

The appearance of the stalk-like portion seen in fig. 48 is explained by the specimen shown in fig. 51. In this the outline of the partially decayed thick wall of the large resting-spore and of the stout hypha which bore it can be traced. The cavity both of the hypha and the spherical spore is filled by a fine mycelium, the spores on which are as yet undeveloped. In the light of this specimen it is easy to understand how the specimen in fig. 48 originated by the complete decay and disappearance of the hypha and the wall of the resting-spore that originally determined the shape of the intrusive mass of fungus.

In other cases vesicles or spores of a similar fungus were developed on the outside of the large resting-spore. A specimen of this nature cut through the middle is shown from the cut surface in fig. 53. The thick wall and the contracted

inner membrane can be traced. The vesicles belonging to the associated fungus are seen covering portions of the thick wall. The same specimen seen from the other side (that is, looking at the outer surface of the wall from which only the central projecting portion is removed) is represented in fig. 52. The groups of vesicles are here seen from above, and not in section. The cavity of the large spore was filled with a fine mycelium bearing small, immature vesicles. Another specimen with the hyphæ and vesicles on the surface is shown in fig. 54.

*Fungus No. 15.* (Figs. 57-71.)

Many of the thick-walled resting-spores of the fungus described above as Fungus No. 2, which, though large, are smaller than those of Fungus No. 3, are also occupied by intrusive fungi, the mycelium of which had produced numerous spherical spores. In so many cases these small spores can be seen to be borne on a mycelium that we are justified in assuming that this was always the case. There is nothing to indicate that they were in any case spores normally developed in, and belonging to, the large thick-walled resting-spore of the original fungus. The enclosed spores may fill the cavity more or less completely, and may also be present in the space between the contracted inner layer and the outer layer of the wall of the large enclosing resting-spore. They may also burst through the wall of the latter or be formed on its exterior. The spores of the intrusive fungus may themselves be occupied by an intrusive mycelium bearing still smaller spores.

While the contained spores thus differ in size, it does not appear possible or desirable to carry out a distinction of form-types on this ground, though it is probable that we are concerned with a number of forms. An adequate idea of the structures in question and the relative positions they occupy will be obtained by referring to a number of examples that are represented in figs. 57-71. These examples could have been considerably extended without, however, substantially adding to our knowledge.

In fig. 57 three resting-spores of Fungus No. 2 are seen in decayed tissue of *Rhynia major*. There is no intrusive fungus to be seen in the spore on the right, but the other two are loosely filled with thin-walled spores. There were only slight remains of the hyphæ which bore these. The middle specimen is more highly magnified in fig. 58. The specimen represented in fig. 59 is similar; it further shows clearly the presence of spores of the intrusive fungus between the layers of the wall of the large resting-spore. The thick-walled spore in fig. 60 is large for Fungus No. 2, and small for Fungus No. 3. It is filled with spores of the intrusive fungus, between which the fine mycelium could be seen, though it is not brought out in the figure. The specimen in fig. 61 similarly shows the spores of the intrusive fungus, some of which are more highly magnified in fig. 62. In all these cases the thin-walled spores approach in size those of Fungus No. 14. This is evident on comparing figs. 49 and 56 with figs. 60 and 62, the magnification in each case being 250 diameters.

The resting-spores of Fungus No. 2 shown in fig. 63 contain an intrusive fungus, the mycelium of which bears spherical spores of a smaller size. Two of the specimens from the group in fig. 63 are more highly magnified in figs. 64 and 65. These figures show that the small spores exhibit differences in size. They also show clearly that the spores are borne on a fine mycelium which may be traceable for a considerable length, or may only remain like a tail or appendage to the spore. Similar remains of the mycelium attached to small spores from another specimen are seen in fig. 66.

The large resting-spore represented in fig. 67, on the other hand, contains a number of rather large thin-walled spores. Within these, again, are small spores that are seen to have belonged to an intrusive fungus by the remains of hyphæ attached to some of them (fig. 68).

The intrusive fungus with its thin-walled vesicles or spores completely fills the oval resting-spore in fig. 69. At one point hyphæ ending in vesicles have burst through the enclosing wall of the large resting-spore (fig. 70). The behaviour of this specimen may be compared with that of the fungus described under No. 11.

Lastly, as in the case of the intrusive Fungus No. 14, related to the larger resting-spores, the thin-walled spores may be formed on the exterior of these resting-spores of type 2. An example of this condition is shown in fig. 71.

#### *Some Other Figured Specimens.*

Small spores similar to those described above as occurring within large resting-spores are also met with distributed through the more decayed fragments of the vascular plants. As a rule, the mycelium is not to be recognised. No advantage is to be gained by detailed descriptions of such remains, which, in some cases, probably belong to forms recognised above. It will be sufficient to illustrate one or two examples.

The small resting-spores shown in figs. 72 and 73 were well defined and rather thick-walled. They were scattered through a decayed stem of *Rhynia Gwynne-Vaughani*. The still smaller dark spores shown in figs. 74 and 75 were similarly distributed through amorphous decayed stems of *Rhynia major*. Among them (fig. 74) were a few larger spherical thin-walled spores. Within these latter there were often some four spore-like bodies without any indication of mycelium. An example is shown in fig. 76.

Spore-like bodies from another decayed fragment of tissue are represented in figs. 77 and 78. The appearance of these is rather different from the well-defined fungal spores, and suggests comparison with small cells of Algæ or Cyanophycææ, forming an irregular colonial mass. Such a possibility, though there is no ground for a definite conclusion, must be borne in mind in considering a number of the less-defined remains in relation to which no mycelium can be demonstrated.

This applies, for instance, to the spherical colonies of small dark cells which are

represented in fig. 79. In this case also it is only possible to point out the resemblance to some Protococcaceæ and Cyanophyceæ, for the peculiar appearance might result from partial decay of a group of fungal spores preceding the preservation.

Though placed for convenience with the fungi, these specimens must be regarded as *incertæ sedis*.

The peculiar spore-like body represented in figs. 80A, 80B, occurred in the decayed cortex of a stem of *Asteroxylon*. The brown wall of the spore on surface view (fig. 80A) showed a reticulate thickening. In section the wall appeared covered by short thin-walled tubes standing at right angles to the surface (fig. 80B). The bases of these tubes seen in optical section give the appearance of the reticulum in the first figure.

The fungi so far described have, as a rule, been situated within the decaying tissues of portions of the vascular plants. Some of them, especially resting-spores, are also met with isolated in the matrix by decay of the surrounding tissues, while type 10 appears to have grown and increased in amount in the amorphous matrix adjoining decaying stems. Hyphæ of fungal mycelium are also met with, branching in the matrix in a fashion that indicates their growth through it rather than their isolation by decay of portions of the vascular plants. No specially characteristic forms of fungi have, however, been met with in the matrix only.

The very well-defined dark spores of medium size and distinctly borne on hyphæ, shown in fig. 81, occurred in the peaty matrix. Somewhat similar specimens have, however, been noted within the decaying tissues.

(b) *Distinction and Description of Species of Fungi.*

The examples described and illustrated above fairly represent the forms of fungi which have come to our notice in studying sections prepared from the Rhynie chert. A survey of them shows that they all consist of branched mycelium bearing terminal or intercalary vesicles or resting-spores. The mycelium is usually and typically non-septate. The hyphæ show a considerable range in diameter, and the vesicles or resting-spores differ widely in size and in the characters of their wall. It must remain an open question to what extent the form-types distinguished above are specifically distinct. The differences in thickness of hyphæ and in size of resting-spore may have been affected by the conditions of life, and perhaps by the occurrence of the fungi in parts of different plants. It does not appear advisable to multiply species or specific names on the imperfect differential characters afforded by fungal remains without any reproductive organs other than chlamydospores. On the other hand, some of the forms are evidently distinct and maintain their characters wherever met with in the deposit. Some are further of interest on account of their regular association with the remains of particular plants or parts of plants. We propose to adopt a middle course and, while not giving names to all the forms recognised above, to distinguish some of the most characteristic of these as species

of the genus *Palæomyces*. This generic name is employed in the comprehensive sense suggested by SEWARD.\* Some of the other types figured may be grouped, on grounds of general resemblance that does not imply specific identity, in relation to those few to which we venture to give names.

The forms which we thus propose to name may be indicated by reference to the numbers used in the preceding descriptions. The specific characters can then be summarised in diagnoses.

The name *Palæomyces Gordoni* will be given to the well-marked and widespread form described as Fungus No. 2 above. The specific name is given to mark the association of Professor W. T. GORDON with the study of the Rhyne chert. As recorded in Part III, we owe to him the unique block of chert containing what we assume to be the reproductive organs of *Asteroxylon*. Under this name also, as *P. Gordoni* var. *major*, the form with similar but larger resting-spores, described as Fungus No. 3 above, may be placed. We may further associate with this species the forms which we do not name, but have distinguished as Fungus No. 1 (hyphal strands) and Fungi Nos. 4 and 5 (thick-walled resting-spores of smaller size).

The name *Palæomyces Asteroxyli* will be given to Fungus No. 7, which is so commonly and typically present in the more or less decayed inner cortex of the rhizomes of *Asteroxylon*. Some other forms with fairly stout hyphæ enlarging into vesicles (e.g. Fungus No. 6) may perhaps be associated with this without placing them under the same name.

On similar grounds, both of structural features and of regular position of occurrence in some rhizomes and stems of *Hornea*, the form described as Fungus No. 8 above may be named *Palæomyces Horneæ*.

There is considerable variety in the forms with relatively small resting-spores or vesicles borne on fine hyphæ. We shall only distinguish and name three of these.

Fungus No. 9 will be named *Palæomyces vestita*. With this we might associate forms that are occasionally met with, and have their larger thin-walled spores sometimes covered in the same fashion by fine hyphæ.

The peculiar and insufficiently known form with hyphæ bursting the surface and terminating in associated pear-shaped vesicles (Fungus No. 13) will be named *Palæomyces Simpsoni*, after Mr SIMPSON, who noticed it and kindly sent us his preparation for study.

The name *Palæomyces agglomerata* is given to Fungus No. 10 as the most characteristic and repeatedly occurring form with fine hyphæ and thin-walled spherical resting-spores. With this may be associated more or less closely, but without bringing them under the same specific name, Fungus No. 11 and Fungus No. 12. Further, the various types of fine mycelium described as Fungus No. 14 and Fungus No. 15, and found as intrusive fungi in the large resting-spores of *Palæomyces*

\* *Fossil Plants*, vol. i, p. 222.

*Gordonii* and *P. Gordonii* var. *major*, have much in common with the type of *Palæomyces agglomerata*, and may be placed beside it without prejudice to their probably including a number of distinct kinds.

Brief diagnoses of these named forms may now be given before entering upon some general considerations on the Rhynie fungi.

The generic name *Palæomyces*\* is employed here as a "useful and comprehensive designation" under which to place fossil fungi, of the precise systematic position of which there is insufficient evidence. It is, therefore, not further defined, but the fungi from the Rhynie deposit that are described below as species of this genus agree in their usually non-septate mycelium bearing spherical or oval vesicles or resting-spores.

In the case of each species a particular slide in the Kidston collection is cited that can be regarded as the type specimen. Most of the species occur more or less frequently in preparations of the Rhynie chert.

*Palæomyces Gordonii*, Kidston and Lang, n.sp. (Pl. I, figs. 6-11. Slide No. 2522.)

Hyphæ usually non-septate (in some cases probably septate); branched; branching without relation to the septa, if present; ranging in diameter from about 6  $\mu$  to 24  $\mu$ .

Resting-spores developed from vesicular swellings on hyphæ; usually terminal; wall thick, differentiated into layers, and usually by contraction of the inner layer giving a double contour to the spore as seen in section. Mature resting-spores show considerable variation in size, but average about 240  $\mu$  by 210  $\mu$ . Occurs in the more or less decayed tissues of *Asteroxylon*, *Rhynia*, and *Hornea*.

*Locality*.—Muir of Rhynie, Aberdeenshire.

*Horizon*.—Old Red Sandstone. (Not younger than the Middle Division of the Old Red Sandstone of Scotland.)

*Palæomyces Gordonii* var. *major*, Kidston and Lang. (Pl. II, figs. 12 and 13. Slides Nos. 2527, 2479.)

Spherical resting-spores; variable in size; up to 550  $\mu$  in diameter; wall about 50  $\mu$  in thickness, stratified; borne on stalk-like portion of hypha about 50-60  $\mu$  in diameter.

Occurs in the more or less decayed tissues of *Rhynia Gwynne-Vaughani* and other plants, and sometimes isolated in the peaty matrix.

*Locality*.—Muir of Rhynie, Aberdeenshire.

*Horizon*.—Old Red Sandstone. (Not younger than the Middle Division of the Old Red Sandstone of Scotland.)

\* SEWARD, *loc. cit.*

*Palæomyces Asteroxyli*, Kidston and Lang, n.sp. (Pls. II and III, figs. 20–28.  
Slide No. 2525.)

Non-septate, branched hyphæ; branches sometimes recurved; ranging in diameter from  $4\ \mu$  to  $20\ \mu$ . Vesicles borne terminally on some of the branches; not separated from the hypha by a wall; attaining a diameter of about  $80\ \mu$ .

Occurs between the cells of the inner cortex of the rhizome and of the axes intermediate between rhizomes and shoots of *Asteroxylon Mackiei*. Also in the more or less decayed tissues of the cortex, and occasionally on the surface of the rhizome in the matrix.

*Locality*.—Muir of Rhyne, Aberdeenshire.

*Horizon*.—Old Red Sandstone. (Not younger than the Middle Division of the Old Red Sandstone of Scotland.)

*Palæomyces Horneæ*, Kidston and Lang, n.sp. (Pl. III, figs. 29–35.  
Slides Nos. 2531, 2532.)

Non-septate, branched hyphæ often with brown walls, attaining a diameter of  $10\text{--}15\ \mu$ ; present in the intercellular spaces of the tissues and also in the adjoining matrix, from which entering hyphæ may be traced. Spherical or oval resting-spores; about  $100\ \mu$  in diameter; with, at maturity, moderately thick, brown walls not differentiated into layers.

Occurs in relation to the surface, and between the cells of some rhizomes and the basal regions of stems of *Hornea Lignieri*.

*Locality*.—Muir of Rhyne, Aberdeenshire.

*Horizon*.—Old Red Sandstone. (Not younger than the Middle Division of the Old Red Sandstone of Scotland.)

*Palæomyces vestita*, Kidston and Lang, n.sp. (Pl. IV, figs. 36–38.  
Slide No. 2454.)

Fine non-septate hyphæ about  $3\ \mu$  in diameter; bearing spherical resting-spores about  $45\ \mu$  in diameter; wall of spore thin, but frequently invested by a close covering of the slender hyphæ. Similar spores of larger size are also met with.

Occurs in decaying tissues, especially of stems of *Asteroxylon*.

*Locality*.—Muir of Rhyne, Aberdeenshire.

*Horizon*.—Old Red Sandstone. (Not younger than the Middle Division of the Old Red Sandstone of Scotland.)

*Palæomyces Simpsoni*, Kidston and Lang, n.sp. (Pl. IV, figs. 45–47.  
Slide No. 2568.)

Characterised by the peculiar grouping of the stalked vesicles, which burst through the surface of a partially decayed stem in oval patches; vesicles widen out

gradually from their hyphal stalks. Diameter of hyphal stalk, up to  $24\ \mu$ . Transverse diameter of vesicle, up to  $100\ \mu$ .

Occurred in a decayed portion of a stem of *Rhynia Gwynne-Vaughani*.

*Locality*.—Muir of Rhynie, Aberdeenshire.

*Horizon*.—Old Red Sandstone. (Not younger than the Middle Division of the Old Red Sandstone of Scotland.)

*Palæomyces agglomerata*, Kidston and Lang, n.sp. (Pl. IV, figs. 39–41.  
Slide No. 2533.)

Fine hyphæ attaining a diameter of  $5\ \mu$ , with terminal or intercalary dilatations giving rise to spherical thin-walled resting-spores  $40\text{--}50\ \mu$  in diameter, that often occur in irregular masses.

Occurs in the tissues of all the vascular plants of the Rhynie deposit, but especially in stems of *Rhynia Gwynne-Vaughani* and in the matrix in connection with them.

*Locality*.—Muir of Rhynie, Aberdeenshire.

*Horizon*.—Old Red Sandstone. (Not younger than the Middle Division of the Old Red Sandstone of Scotland.)

From the systematic point of view the fungi which have been described above, and to some of which specific names have been given, add little to our knowledge. While providing beautifully preserved and abundant examples of mycelium and resting-spores in the decaying parts of plants in the silicified peat, their type of construction is, on the whole, similar to those fungi already known from Carboniferous rocks. Their Early Old Red Sandstone age, however, gives them an increased interest.

The general characters of these fungi suggest a systematic position with the Phycomycetes, and probably (though there is no definite evidence for this) with the Oomycetes. The mycelium seems to have been typically non-septate. The one example in which transverse septa were fairly frequent and well marked appears exceptional among the numerous specimens examined, and this mycelium resembles in other respects the non-septate mycelium found in a corresponding position. The formation of septa, in addition to those formed in the development of reproductive organs, is well known to occur among existing Phycomycetes, and we do not feel justified in laying stress on this character by itself. While characteristic asexual or sexual reproductive organs are wanting, the type of resting-spores (chlamydo-spores), which, when immature, often appear as terminal vesicles, can be best paralleled among existing Phycomycetous fungi.

The only systematic conclusion that we appear to be warranted in drawing from the rich assemblage of fungal mycelia, vesicles, and resting-spores in the Rhynie peat is that the occurrence of Phycomycetes already established for the

Permo-Carboniferous period can be extended back to the Early Devonian. There is no satisfactory evidence of the existence of Eumycetes, although, in the light of the demonstration of septate mycelium, the question of their presence must be left to some extent open.

Since the fungi of the Rhynie peat show only hyphæ, vesicles, and resting-spores, any exhaustive comparison with other fossil and living forms would be of little value. It is only necessary to make clear some general lines of comparison.

As already pointed out, these fungi, though more abundant and perfectly preserved, resemble the fungal remains known from Permo-Carboniferous rocks. Some of these have had names given to them, while the features of others are sufficiently known by descriptions and figures. Attention has been directed by a number of investigators to the hyphæ and resting-spores found in connection with decaying vegetable remains in the coal-balls. The Rhynie fungi are similar in general type to these. Thus the groups of spores developed from the intrusive mycelium in the large resting-spores of *Palæomyces Gordoni* and *Palæomyces Gordoni* var. *major* may be compared with the fungal spores filling certain megaspores of *Lepidodendron* as described by WILLIAMSON.\* A portion of hypha attached to one of the spores of the intrusive fungus is indeed shown in WILLIAMSON'S drawing.†

A number of forms of palæozoic fungi which have been described and named by various observers are collected by MESCHINELLI,‡ to whose work it will be sufficient for our purposes to refer. Leaving aside more problematical remains, the general similarity of the forms described by MESCHINELLI as Phycomycetes, under the names of *Palæomycites gracilis*, *Palæomycites majus*, *Peronosporites antiquarius*, *Protomycites protogenes*, and *Oochytrium Lepidodendri*, to some of the Old Red Sandstone fungi described above will be evident. In particular, we may point out the resemblance between the hyphæ and vesicles or spores of *Peronosporites antiquarius* and those of *Palæomyces Asteroxyli* and *Palæomyces Gordoni*; between *Palæomycites protogenes* and *Palæomyces Gordoni*, as regards the double contour of the spore; and between the fine hyphæ attached to small spores of *Oochytrium Lepidodendri* and the intrusive mycelium and spores of some of the fungi described under No. 14 above. The remains of fine hyphæ forming appendages to the spores are characteristically similar in the latter case.

It is not easy, in view of the merely vegetative growth-forms in which the fungi of the Rhynie peat occur, to go far in comparing them with existing fungi. As already pointed out, it is impossible in the absence of distinctive reproductive organs even to refer them to a particular group of the Phycomycetes. The characters of the mycelium and resting-spores suggest comparisons with Saprolegniaceæ, Pythiaceæ, and Peronosporaceæ. In various forms of these (and in other fungi) the mycelium is

\* *Annals of Botany*, vol. i (1888), p. 315.

† *Loc. cit.*, pl. xviii, fig. 15.

‡ *Fungorum Fossilium Omnium Iconographia*, Vicetie, MCMII.

known to develop vesicular dilatations, and thin or thick-walled gemmæ or resting-spores, though rarely in the profusion shown by these extinct fungi.

A specially instructive comparison may be made with the fungus distinguished by C. WEST as *Stigeosporium*,\* which occurs in the living roots of a number of Marattiaceæ. The non-septate hyphæ of varying degrees of thickness, the formation of vesicles and their transformation into thick-walled resting-spores, the differentiation of the wall of which shows an approach to a double contour, are points of resemblance. WEST infers, although only vegetative mycelium and chlamydo-spores were available, a position in the Oomycetes, and compares the resting-spores of *Stigeosporium* with those described for some species of *Phytophthora*.

Terminal or intercalary vesicles and thick-walled resting-spores borne on non-septate hyphæ are also met with in a number of other fungi which are only known as endotrophic mycorrhiza.† The further fate of such vesicles or chlamydo-spores is unknown, even in the case of these existing forms, while in them also other reproductive organs are wanting. It is, therefore, unnecessary to enter into detailed comparisons, and a general reference to such mycorrhizal fungi will be sufficient.

The comparisons last made naturally lead to the consideration of the question whether there is any evidence of an association between the fungi and the Vascular Cryptogams in the Rhyne peat suggesting mutualistic symbiosis or mycorrhiza. This possibility cannot be dismissed, although it is difficult to obtain evidence that is not open to other interpretations in dealing with the more or less decayed plant-remains in the deposit.

It appears to be beyond doubt that many of the fungi were living as saprophytes and are associated with the decay of the tissues in which they are found. This is clearly the case with the strands of hyphæ replacing the phloem of *Asteroxylon* and with such fungi as *Palæomyces Gordoni* that occur in various parts of the different vascular plants. It also holds for others like *Palæomyces agglomerata*, *Palæomyces vestita*, and most of those to which names have not been given, although they may not be so generally distributed. There remains the possibility, however, that some of the plants contained a mycorrhizal fungus when they were alive, and further that some of the fungi that were evidently living as saprophytes in the peat might have come from mycorrhizal fungi taking on a saprophytic mode of life after the death of the plant-tissues.

Certain fungal types are regularly found in association with particular vascular plants. Thus *Palæomyces Horneæ* is found in a number of specimens of the rhizomes and the basal region of the stems of *Hornea*. The hyphæ are intercellular, and their connection with fungus outside the rhizome has been followed. The fact that other well-preserved rhizomes of *Hornea* are without any trace of this fungus is,

\* *Ann. Bot.*, vol. xxxi (1917), p. 77.

† For numerous figures cf. JANSE, *Ann. Jard. Bot. Buitenzorg*, xiv (1897), p. 53, and various descriptions of mycorrhizal fungi, especially those occurring in Lycopodiaceæ and Ophioglossaceæ.

however, against interpreting the relation as mycorrhizal. The evidence in this case is on the whole more consistent with a saprophytic fungus selecting for its growth certain tissues or regions of a plant.

The fungus that has been named *Palæomyces Asteroxylti* is very regularly found in the inner cortex of rhizomes of *Asteroxylon* and of the basal regions of stems with the transition structure. Some rhizomes, especially finer branches, are, however, met with apparently free from the fungus. The localisation of the fungus to the intercellular spaces of the broad inner cortex, leaving both the outer cortex and the phloem free, is in support of the view that it was mycorrhizal. It must be borne in mind, however, that a similar regional preference has been seen in the case of other fungi in the inner cortex of stems of *Rhynia Gwynne-Vaughani* and *R. major*, where these occasional inhabitants were clearly saprophytic. The regularity of the association in *Asteroxylon* and its occurrence in the subterranean regions of the plant appear to justify us in keeping open the question of its having been normally associated with the plant when alive. In this case also, although the evidence of a mycorrhizal relation is considerably stronger, it does not amount to proof, and it is clear that the fungus is often associated with the breaking-down of the inner cortex of the rhizomes; its original intercellular distribution is then, of course, lost.

The case of the two species of *Rhynia* is of a rather different nature.\* There is no doubt that the active growth of various fungi with evident mycelium bearing vesicles or resting-spores was here saprophytic. The distribution and appearance of the layer of cells with very persistent dark contents immediately below the outer cortex suggests, however, the possibility that this region might have contained a symbiotic organism. The distribution of this layer is shown for *Rhynia major* in Part I, figs. 21 and 22, and for *R. Gwynne-Vaughani* in Part I, fig. 59. Against such an interpretation of the contents is the fact that this layer is marked in the stouter stems, and not in the rhizomes. The contents are not evidently mycelial when carefully examined. In some cases, however, appearances have been noted that would be consistent with the presence of a very fine and closely packed mycelium. Figs. 82-84 are of such a specimen, and to some extent indicate the appearance and the difficulty of coming to a definite decision on the question. It is suggestive that such fungal growths as that shown in fig. 43 often, though not always, originate in the position of this layer of cells (*cf.* p. 862); this would be equally consistent with the evident fungus being a further development of a mycorrhizal organism, or being a purely saprophytic fungus selecting for its growth this peculiar layer of cells. Thus in the case of *Rhynia* also the only conclusion at present seems to be that proof of the existence of mycorrhiza is wanting, though there are grounds for further enquiry into the question.

As already mentioned, the inference that most of the fungi in the deposit were living as saprophytes seems to be well justified. It is difficult to draw any sharp line

\* *Hornea* showed corresponding structures to those to be described, but the preservation was poor.

between the occurrence of these fungi and the other cases which at first sight appear open to the interpretation of a mycorrhizal association. In all of the latter the evidence appears to be much weaker than was the case for the relation of some palæozoic plants to fungi which has been interpreted as probably symbiotic.\* Only convincing evidence from structural relations is admissible in a physiological question such as that under discussion. The appearances in the Rhyne plants do not afford such evidence, although they leave open the possibility that a mycorrhiza may have been present in the actively living plant.

## 2. SCHIZOPHYTA.

A few remains that belong to either the Bacteria or the Cyanophyceæ are placed together in this section, on account of the impossibility of determining whether certain filamentous forms were green or colourless during life.

### *Schizophyta No. 1. Unicellular Bacteria.* (Pl. VII, fig. 85.)

There is no reason to doubt that unicellular Bacteria were present, often in abundance, throughout the partially decayed mass that is preserved in the Rhyne chert. The finely granular nature of the matrix, however, renders their recognition problematical. This applies even to appearances strongly suggesting colonial masses of Bacteria that occur free or coating vegetable fragments or fungal hyphæ in the peaty matrix. Such appearances closely resemble the mode of occurrence of Bacteria in some processes of decay at the present time.

One illustrative example is represented in fig. 85. The irregularly lobed masses there shown occurred in groups in the matrix of a block of the chert that contained the algal remains to be described in the following section. They are so like the well-defined bacterial colonies or zooglæal masses that appear when Algæ are decaying in fresh or salt water that they may reasonably be regarded as of this nature. The granular character would be due to the unicellular bacteria. For comparison unstained colonies of such a recent bacterium are represented to the same scale in fig. 86.

### *Schizophyta No. 2.* (Pl. VIII, figs. 87 and 88.)

The organism represented in figs. 87 and 88 occurred most abundantly in certain blocks of the chert at the upper limit of the *Rhynia Gwynne-Vaughani* peat that formed the base of Bed A"1. It there formed a loose felt of fine tubular filaments, about 2  $\mu$  in diameter. Groups of fungal spores are entangled in the meshes of the felted mass, but seem to have nothing to do with the organism in question. The filaments might be slender fungal hyphæ, but they have not been observed to branch, and their curvature and arrangement is much more suggestive of the growth of one of the Trichobacteria than of a fungus. They may represent the sheaths of one of

\* WEISS, *Ann. Bot.*, vol. xviii (1904), p. 255; OSBORN, *ibid.*, vol. xxiii (1909), p. 605.

the Filamentous Bacteria. No satisfactory evidence of septation or of the presence of bacterial cells within the tubular sheath has been obtained. Under certain conditions of preservation the latter contains dark granules, but the arrangement of these is too irregular to afford a safe indication of any original structure.

The organism is so well marked in appearance and mode of occurrence that it is recorded and figured here, but, as pointed out above, its systematic position must be regarded as somewhat uncertain. It is suggested below (p. 876) that it may be referred to provisionally by the name *Archæothrix contexta*.

*Schizophyta* No. 3. *Archæothrix oscillatoriformis*. (Pl. VIII, figs. 89 and 90.)

A remarkably well-preserved organism that can only be placed in the Schizophyta is represented in figs. 89 and 90. It was found in a large cavity due to decay in a stem of *Rhynia Gwynne-Vaughani* in the form of a number of slender unbranched filaments. Two groups of these are seen at *a* and *b* in fig. 89, and above group *a* a long undulating filament is very clearly shown. A portion of this latter filament is represented more highly magnified in fig. 90. The way in which some of the filaments were curved back on themselves contrasted with the behaviour of fungal hyphæ, some of which were also present in the cavity. The filaments (fig. 90) were divided into numerous short discoid cells, the protoplasts of which have persisted and been preserved.

The structure of this remarkable organism may be most closely compared with such existing plants as slender forms of *Oscillatoria*; it agrees with these in the short disc-like cells and in the curvature of the unbranched filaments. It is, however, also comparable with the slender colourless filaments of such existing Bacteria as *Beggiatoa*, and it is generally recognised that there is much in common between the Oscillatoriaceæ and the Beggiatoaceæ. Though it is, of course, impossible to tell whether the fossil plant was green or colourless when alive, its systematic position appears to be clear. It is noteworthy that in this specimen it is the protoplasts or cell-contents that have persisted—a mode of preservation that is unlike that of the fungi in the same bed of the deposit. This feature as well as the general appearance seems to be in favour of regarding this organism as one of the Cyanophyceæ.

*Archæothrix*, n.g., Kidston and Lang.

Slender unbranched filaments suggesting close comparison with Filamentous Cyanophyceæ or Filamentous Bacteria.

*Archæothrix oscillatoriformis*, n.sp., Kidston and Lang. (Pl. VIII, figs. 89 and 90.  
Slide No. 2542.)

Unbranched filaments, often curved; about 3–4  $\mu$  in diameter. Within a sheath-like outer wall are the preserved protoplasts of the small discoid cells.

Occurs in a cavity of a decayed stem of *Rhynia Gwynne-Vaughani* in the lowest bed (A<sup>n</sup>1) of the deposit.

*Locality*.—Muir of Rhynie, Aberdeenshire.

*Horizon*.—Old Red Sandstone. (Not younger than the Middle Division of the Old Red Sandstone of Scotland.)

The filamentous organism described as Schizophyta No. 2 above, may provisionally be placed under the same generic name as *Archæothrix contexta*.

### ALGITES, Seward.

1894. *Algites*, Seward, *Catal. Mesoz. Plants in British Museum*, pt. i, p. 2.

#### 3. ALGITES (PALÆONITELLA) CRANII, n.sp. (Pl. IX, figs. 98-104.)

We give this name to some fragmentary remains of a plant that was clearly an Alga. While, in the absence of distinctive reproductive organs, it is impossible to determine its systematic position, certain characters of the vegetative organs will be seen to present resemblances to those found in existing Characæ.

The name is applied in the first instance and the species is founded on specimens of septate filaments, occasionally with evidence of the existence of nodal discs of small cells, which have been met with in a few blocks of the chert. These remains are of the type represented in figs. 98-104 and text-figs. 6-11.

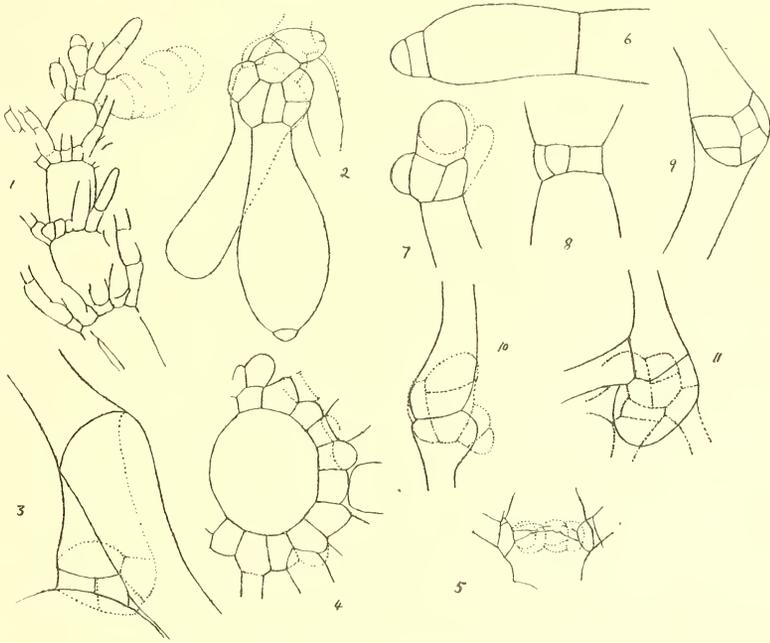
We associate with these remains some remarkable specimens of more uncertain nature found in a loose block of the chert by the Rev. Mr CRAN of Skene in preparations he had made while studying the animal remains in the chert. Mr CRAN generously handed his preparations and drawings to us for description, and we have great pleasure in naming after him the undoubted algal remains mentioned in the preceding paragraph. The actual specimens he discovered (figs. 91-97 and text-figs. 1-5) are not treated as the type but, for the present at least, are regarded as to some extent *incertæ sedis*; they are, however, with some confidence associated with *Algites Cranii*.

In the same way we provisionally place in association with this species some peculiar globular or oval vesicles and filaments accompanying these (figs. 105-108). These are of interest and require to be recorded, but their nature is still uncertain. They were obtained from blocks removed from the bed *in situ*.

The type specimens will first be described, and then these specimens of more or less uncertain affinity, but of morphological interest, will be dealt with.

The general appearance of a portion of a section showing a characteristic group of the remains of *Algites Cranii* in the peaty matrix is represented in fig. 98. The prominent structures are stout septate filaments with dark contracted remains of the protoplasmic contents of the cells. Some of the filaments are more highly magnified in fig. 99. The tip of a filament is sometimes seen as at *a* in fig. 98; it ends in a

dome-shaped cell, and was evidently of limited growth (*cf.* figs. 99 and 100 and text-fig. 6). No branching of the simply septate filaments has been seen. In some specimens, however, as at *b* in fig. 98 (*cf.* fig. 101 and text-fig. 7) a node of small cells is found in the course of a filament, and there are indications of the nodal cells



FIGS. 6-11 show details of specimens of *Algites (Palaeonitella) Cranii*; FIGS. 1-5 are of some specimens received from Mr CRAN which we place with this plant. Cell-walls shown in another focal plane are dotted.

1. Outline of the verticillately branched axis represented in figs. 91-93. After Mr CRAN'S drawing.  $\times 155$ .
2. Outline of the specimen represented in fig. 95. After Mr CRAN'S drawing.  $\times 125$ .
3. Outline drawing of portion of the specimen represented in fig. 96.  $\times 165$ .
4. Outline drawing of the specimen represented in fig. 94.  $\times 165$ .
5. A specimen that may be a longitudinal section of a node similar to those in text-figs. 1 and 4. After Mr CRAN'S drawing.  $\times 115$ . Slide 2573.
6. Apex of filament shown in fig. 98 at (*a*).  $\times 165$ .
7. Outline drawing of nodal disc shown in fig. 98 at (*b*) and in fig. 101.  $\times 165$ .
8. Outline drawing of another node from the same slide.  $\times 165$ .
9. Outline drawing of the rhizoid node shown in fig. 103.  $\times 165$ .
10. Outline drawing of the rhizoid node shown in fig. 104.  $\times 165$ .
11. Outline drawing of another rhizoid node.  $\times 165$ . Slide 2546.

growing out as branches. In text-fig. 8 a second example of a shallow nodal disc separating two of the large cells is represented. Another case of the existence of a node of small cells accompanied by branching is seen at *c* in fig. 98 (*cf.* fig. 102); there are certain resemblances in this specimen to the rhizoids to be described

below. Lastly, at *d* in fig. 98 there is a thin-walled globular vesicle, unfortunately ill-preserved, but apparently attached to a filament. Attention is directed to it, since similar structures occur in the neighbourhood of filaments of the Alga in several blocks of the chert from different levels in the deposit, and globular vesicles are found in the groups of remains described below.

Traversing the peaty matrix of the block from which fig. 98 was obtained, several examples of structures which we can only interpret as rhizoids were met with. Two of them are represented in figs. 103 and 104 and text-figs. 9 and 10. The long tubular cells are separated from one another by an oblique septum, the region of junction being more or less enlarged. In relation to the septum an irregular node of small cells was usually developed (fig. 104). These structures present a general resemblance to the peculiar rhizoids of the Characeæ. Another example is represented in text-fig. 11.

We feel no hesitation as to the vegetable nature of the remains described above, nor as to their belonging to an Alga. The simple filaments might be comparable to a number of Algæ, but the presence of occasional nodal discs and the appearance of the rhizoids strongly suggest more special comparison with the Characeæ.

*Remains provisionally associated with Algites Cranii.*

(Pl. VIII, figs. 91-97; Pl. IX, figs. 105-108.)

As mentioned above, we received certain remarkable specimens from the Rev. W. CRAN, B.D., of Skene. These occurred in the cloudy matrix of a loose block of the chert containing *Rhynia Gwynne-Vaughani* and animal remains.

The first specimen shown to us by Mr CRAN consisted of a small axis embedded in the matrix of a rather thick section. The thickness had the advantage of leaving the small "shoot" intact, but made observation and figuring difficult. The morphology of the specimen is well shown in Mr CRAN'S drawing reproduced in text-fig. 1. This shows an axis formed of four internodal cells separating as many nodes; these are marked by the whorls of more slender and sometimes septate appendages borne at each. In relation to, and possibly in continuity with, the upper end of the specimen is a peculiar row of cell-like structures; this is one of the difficulties in the interpretation of this specimen.

The appearance of the specimen is further shown in figs. 91 and 92 on Pl. VIII. These are magnified 100 diameters, and show the small specimen as it lies in the cloudy matrix. The plane of focus in fig. 91 brings out the internodal cells, while fig. 92 shows the whorled appendages at the nodes better. A portion of the specimen showing the appendages at two of the nodes is more highly magnified in fig. 93.

Another very instructive specimen discovered by Mr CRAN is represented on Pl. VIII, fig. 94, and text-fig. 4. This can be readily placed in relation to the preceding specimen as a node with the bases of the verticillate branches as seen in

cross-section. The specimen is incomplete on the upper side in the figure, but shows all the essential parts. Centrally is the outline of the main axis with a diameter of  $140 \mu$ . This is clothed by a zone of small cells, in relation to which the bases of a number of branches can be seen.

It is tempting to recognise in these specimens parts of small axes with a construction like the existing Characeæ. This is not improbably their nature, but some suspension of judgment is perhaps desirable until further specimens are found. This also applies to another specimen represented from Mr CRAN'S drawing in text-fig. 5. It may perhaps be the longitudinal section of a node similar to those in the two preceding specimens, but its nature does not appear to us to be sufficiently clear to do more than record it.

Some other remains now to be described were found in Mr CRAN'S sections in close association with the above specimens, and probably belong to the same organism, though there is no direct proof of this.

The specimen shown in fig. 95 had penetrated, or at least was situated beneath, the surface of a decayed stem of *Rhynia Gwynne-Vaughani*. Its structure, which is not shown in any one plane of focus, is brought out by Mr CRAN'S drawing in text-fig. 2. There appears to have been an elongated internodal cell widening out to a nodal disc of small cells. The axis possibly continued beyond this, while laterally from the nodal disc there arose two wider appendages, one of which was swollen distally. We tentatively suggest a comparison of this specimen with the node of a Characeous rhizoid which bears bulbils.

The specimen in fig. 96 may be placed in relation to this. Here the continuity of the slender tubular axis of the rhizoid (?) can be traced. The segment above the oblique septum bulges out, and appears to have formed several cells. It continues into the large globular vesicle (bulbil ?), the distal portion of which is wanting at the edge of the section. A shallow nodal disc, probably the basal group of cells in optical section, is evident at the base of this vesicle, which we thus tentatively interpret as a bulbil attached to a rhizoid. The details of the region of attachment of the vesicle are shown in text-fig. 3.

In fig. 97 a similar globular structure is seen lying free in the matrix of the chert. The thickness of the preparation allows it to be viewed as a solid object. To the right a node-like disc of cells is attached to the globular vesicle, and from some of the cells of this nodal disc slender tubular filaments appear to have grown out. It is possible to regard the vesicle as borne laterally on the filament, but the above interpretation seems more probable. In that case the remarkable resemblance which the specimen presents to a germinating bulbil of *Chara aspera* or *Lamprothamnus* is of interest in considering a group of remains which we appear to be forced to compare with Characeæ.

In connection with the specimens last described which came from Mr CRAN'S block, the assemblage of imperfectly preserved remains of uncertain nature shown in

fig. 105 is of interest. This is a fair sample of what has been met with at certain spots in the upper region of the *Rhynia Gwynne-Vaughani* peat in Bed A''1. Stout wide tubes with contracted contents are found in transverse and longitudinal section. The most prominent objects, however, are large oval or globular vesicles that are usually isolated in the matrix, but have been seen borne on, or connected with, some of the tubes. The vesicles are often single, but may have outgrowths from the base, and so be associated in pairs (fig. 107). In other cases they form rows of two or three (figs. 105 and 106), and sometimes indications of a node separating the vesicles have been seen. The thin wall of the vesicle is sometimes smooth (fig. 107), but in other specimens appears papillate (fig. 106, to the right.)

The specimen shown in fig. 108 was found in the peat among such vesicles. In spite of its advanced decay, rendering the outline faint, an organisation of the tubular structures into an internode separating two nodes with verticillately arranged appendages can be clearly traced. This specimen also shows the tubular filaments with their contracted contents.

It seems significant that globular, vesicle-like structures were met with in relation to the specimens we have described as *Algites Cranii* (cf. fig. 98), and also in association with this plant in blocks of the chert from other beds. In addition, we have the globular vesicles in association with Mr CRAN'S specimen (figs. 96 and 97). While it cannot be stated definitely that these bodies are all of the same nature, it is a possible tentative interpretation that they all belonged to the same type of plant and were bulbils serving for vegetative reproduction like those in some Characeæ.

While the various remains described above differ from one another, they do so in a way that is consistent with their all being parts of the same plant. Their association is in favour of such an interpretation, and this is supported by the fact that we have in one group of existing Algæ much the same sort of range in morphological construction in different regions of the plant. The verticillately branched axes in figs. 93 and 108 and the nodal arrangement in fig. 94 resemble broadly what is found in the "shoots" of the Characeæ. The simply septate filaments in figs. 98 and 99 with occasional nodes (fig. 101) can be paralleled with the "leaves" of some Characeæ. The rhizoid structure (figs. 103 and 104) is also only to be compared with that in the same group. Lastly, the large globular unicellular structures, including the specimen with an attached node in fig. 97 that appears to be germinating, find a general but fairly close parallel in the type of bulbil present in *Chara aspera*\* and *Lamprothamnus*.†

These resemblances taken collectively seem to us of real significance, and are difficult to explain without assuming that they indicate relationship. Since, however, no specimen of the characteristic reproductive organs of the Characeæ has as yet been found in the Rhynie deposit, the question of the systematic position of *Algites Cranii*, and the other remains we have provisionally associated with it, is

\* Cf. GIESENHAGEN, *Flora*, lxxxii (1896), p. 381.

† Cf. M'NICOL, *Ann. Bot.*, vol. xxi (1907), p. 61.

better for the present regarded as an open one. That, however, in a number of respects these remains resemble the isolated existing group of the Characeæ has been made evident in the description and discussion above. In this connection it should be borne in mind that structures suggestively like the oogonia\* of a Characeous plant have been recorded from Devonian rocks in America.

We have indicated the uncertainty that must still exist as to the systematic position of the remains under consideration by placing them for the present in the comprehensive genus *Algites*. On the ground, however, of various features of the vegetative structure that suggest that we are probably dealing with a Characeous plant with unarticulated internodal cells, we provisionally suggest the generic name *Palæonitella*. We thus for the present name the plant *Algites (Palæonitella) Cranii*; the name *Palæonitella* may be definitely adopted if the systematic position of the plant is confirmed by the discovery of reproductive organs, or abandoned should these show that the affinities of the plant are not with the Characeæ.

*Algites (Palæonitella) Cranii*, Kidston and Lang, n.sp. (Pl. IX, figs. 98-104, and text-figs. 6-11).

Septate filaments composed of cells with fairly thick walls and contracted dark contents. Tip of filament ending in a dome-shaped cell. Sometimes a short node of small cells occurs separating two of the large cells. Branching from cells of the node. Rhizoids (?) with elongated tubular cells separated by oblique septa, in relation to which there is an irregular node of small cells. Large vesicles associated with the remains.

Occurs in the matrix of the peat in certain beds of the Rhynie deposit. The rhizoid-like structures may be within decayed tissues of plant-fragments.

*Locality*.—Muir of Rhynie, Aberdeenshire.

*Horizon*.—Old Red Sandstone. (Not younger than the Middle Division of the Old Red Sandstone of Scotland.)

*Incertæ sedis, but associated with Algites Cranii as probably belonging to it.*

(Pl. VIII, figs. 91-97, and text-figs. 1-5.)

Small axis with internodal cells and whorls of appendages at the nodes. Rhizoid-like structures and spherical bulbils (?).

(Pl. IX, figs. 105-108.)

Tubular filaments with contracted contents; sometimes showing an internodal cell separating nodes with verticillate branches. Globular or oval vesicles (bulbils ?).

\* KNOWLTON, *Amer. Journ. Science*, vol. xxxvii, p. 202; SEWARD, *Fossil Plants*, vol. i, pp. 225-226.

## NEMATOPHYTON, Penhallow.

1859. *Prototaxites*, Dawson, *Quart. Journ. Geol. Soc.*, vol. xv, p. 484.1871. *Nematoxylon*, Dawson, *Geol. Survey of Canada*, "Fossil Plants of Devonian and Upper Silurian Formations," p. 20.1872. *Nematophycus*, Carruthers, *Monthly Micros. Journ.*, p. 172.1888. *Nematophyton*, Penhallow, *Trans. Roy. Soc. Canada*, vol. vi, section iv, p. 36.

## 4. NEMATOPHYTON TAITI, n.sp., Kidston and Lang.

The discovery in the Rhynie chert of a fragment of tissue, the structure of which agrees closely with that of plant-remains known from the Silurian and Devonian formations under the names *Prototaxites*, *Nematoxylon*, *Nematophycus*, or *Nematophyton* adds to the interest of the deposit. This small fragment only appears in two successive sections of a block from Bed A"1; it measures only  $3 \times 2$  mm. The characteristic structure is, however, well shown, the tissue being composed of systems of wide and of narrow tubes; the differences from the specimens on which other species have been founded are merely in details, such as those on which these species are distinguished. This is, we believe, the first record of *Nematophyton* from the Old Red Sandstone of Scotland. We have pleasure in naming this species *Nematophyton Taiti*, after Mr DAVID TAIT, who superintended the excavations at the Muir of Rhynie that resulted in the discovery of the silicified peat-bed *in situ*.

We associate with this fragment, without giving it a separate name, another slightly larger portion of a plant which occurred at the same level in the same block, but was cut in two other sections of the series. This second fragment, which was only about 4 cm. distant from the fragment showing the typical structure of *Nematophyton*, is a portion of the peripheral region of a cylindrical structure. The structural differences it exhibits from the other fragment can reasonably be explained on this ground. Though there is no proof of continuity, we feel justified in placing it with the first specimen under the same name. The two specimens will, however, be described apart, and the figures will enable the reader to form his own opinion as to their belonging to the same plant.

If, as we believe, the second fragment shows the peripheral region of a plant the central portion of which had the typical *Nematophyton* structure, it is a welcome addition to our knowledge of this remarkable genus. It is in any case a portion of the peripheral region of a plant of a similar type of construction.

The two specimens may now be described in detail, taking them in the order in which they are mentioned above.

One of the two sections with the typical structure of *Nematophyton* is slightly larger than the other and shows the tissue better preserved. The irregular edges of the fragment are decomposed and covered with a granular mass that is possibly of bacterial origin. The greater part of the better section is shown magnified 50 diameters in fig. 109. This figure shows that the wide tubes making up the bulk

of the tissue are on the whole cut transversely in this section, which may be presumed to be transverse to the long axis of the portion of the plant from which the fragment comes. A number of approximately circular areas from which the wide tubes are absent are shown; for these the term "medullary spots"\* may be employed. A portion of the section is magnified 100 diameters in fig. 110, and two other portions are magnified 250 diameters in figs. 111 and 112. The last-named figure shows a portion of one of the medullary spots surrounded by the tissue formed of large tubes.

The relatively large tubes show considerable range in size, but those of different diameter are mixed together and not arranged in concentric zones as in *Nematophyton Loganii*. The largest have a diameter of 52  $\mu$ , while the smaller ones measure only 20  $\mu$ . They are frequently contiguous, often forming rows or small groups, while at other places they are distinctly separated from one another. The intervening spaces, like the medullary spots, were occupied by the system of fine tubes or hyphæ to be described below.

The walls of the larger tubes are usually very thick and often appear thicker at one side than at the other. Thus in a tube 34  $\mu$  in diameter the thickness of the wall ranged from 4  $\mu$  to 7  $\mu$ . Another tube 48  $\mu$  in diameter had the wall 14  $\mu$  thick. Other tubes had thinner walls, the wall of one with a diameter of 20  $\mu$  being only 2  $\mu$  thick. The tubes thus vary from 20–52  $\mu$  in diameter, with a wall-thickness varying from 2  $\mu$  to 14  $\mu$  or more. The apparent thickness of the wall may have been affected by the state of preservation of the tube.

The tubes so far described are cut transversely, but others lie obliquely and are therefore seen from the side or in longitudinal section as they lie between the other tubes. These obliquely running tubes are sometimes relatively narrow, down to 12  $\mu$ , but belong to the system of relatively wide tubes. Some of them can be traced into the medullary spots.

Where the relatively large tubes are not in close contact, and especially in the areas of the medullary spots, there is evidence of the presence of a second system of delicate tubes of about 10  $\mu$  in diameter. In most places between the wide tubes and in most of the medullary spots the tissue formed by the narrow tubes has lost its structure and is either amorphous or replaced by a pseudo-cellular structure. In one or two of the medullary spots, however, the delicate tubes could be more or less clearly followed, and we have no doubt that they were originally present in the corresponding situations from which they have decayed.

It will be seen that, small as this specimen is, it shows all the types of tissue described for other species of *Nematophyton*.

It is not necessary or desirable to press the description of the tissues of this small fragment of *Nematophyton* further. It is sufficient to be able to recognise that it agrees with other specimens of this genus in the absence of true tissues such

\* PENHALLOW, *Ann. Bot.*, vol. x, p. 144, 1896.

as result from cell-division and in being largely composed of relatively wide tubular elements, between which, and most characteristically in the medullary spots, there is a system of delicate, narrow, interlacing tubes.

The Rhynie species differs\* from *N. Loganii* in the absence of radial bands and the presence of "medullary spots." In *N. Storriei*, although there are "medullary spots," the large tubes are always separated by a slight space, are smaller, and have thinner walls. With *N. Ortoni* it agrees in the presence of "medullary spots," but the wide tubes of that species are larger, attaining a maximum diameter of 67  $\mu$ , and are more uniform in size. The thick walls of the Rhynie species show some similarity to those of *N. crassum*, but the wide tubes are larger in the Scottish species and the cavity is always prominent.

From *N. laxum* and *N. tenue*, as described by PENHALLOW, it appears to be distinguished by several characters. The preservation of these forms and of *N. Hicksii* and *N. Dechenianum* is, however, too imperfect to admit of detailed comparisons.

Such specific distinctness, interesting as it is, is secondary in importance to the recognition in this deposit of an example showing the characteristic construction of this type of plant. The diagnosis will be given after the description of the second fragment.

Of the second fragment there were also two sections, one of which shows the tissues rather better preserved than the other, though both are instructive. The greater part of the better section is represented, magnified 30 diameters, in fig. 113. As this shows, the fragment includes a portion of the outer surface of the plant and the tissue lying beneath this. The curvature of the surface indicates that the part of the plant was cylindrical (or less probably spherical). If we assume it to have been cylindrical, the curvature indicates a diameter of about 1.2 cm.

The following structural regions can be distinguished proceeding from the outer surface inwards: (a) a narrow, clear, structureless zone; (b) a zone about 1 mm. in depth, composed of tubular filaments standing at right angles to the surface; (c) an inner region in which the tubes or filaments run irregularly; these tubes are continuous with those of zone b. A number of small areas of different texture, that appear as dark spots in the figure, are distributed through this region. The same zones are shown rather more clearly in fig. 114.

The chief structural component of the inner tissue (zone c) has the form of branched tubes or filaments running irregularly in all directions and crossing one another so as to give the effect of a reticulate structure (figs. 115 and 116). These filaments when best preserved stand out by reason of their brown colour and homogeneous appearance. This seems referable to a preservation of the contents rather

\* It will be sufficient to give a general reference to the diagnoses of *N. Loganii*, *N. Hicksii*, *N. crassum*, *N. laxum*, and *N. tenue* in PENHALLOW'S paper (*Trans. Canad. Roy. Soc.*, vol. vii, 1889, p. 28); to that of *N. Ortoni*, in a paper by the same investigator (*Ann. Bot.*, vol. x, 1896, p. 41); and to that of *N. Dechenianum*, in the paper by SOLMS (*Jahrb. d. k. preuss. Geol. Landesanstalt*, 1894).

than of the walls of the tubes.\* The cylindrical brown threads may appear as if cracked across, but there is no satisfactory evidence of the filament having been septate. At places a beaded appearance, possibly due to contraction of the contents, is found. Careful search reveals tubes in which the wall is preserved and which, therefore, appear wider than the brown threads. There has been much breaking-down and rearrangement of the substance during preservation, and the clear intervals or matrix between the tubes often exhibits pseudo-cellular structure; this is most marked where the decay is most advanced and the tubular structure has disappeared.

A feature of considerable interest in the preservation of some of the tubes is the appearance of a fine spiral marking. This runs round the inside of the thick wall of the tube. In favourable examples (fig. 118) the thickness of the wall can be traced, and the spiral marking seen in section to be due to a regular ridging of the innermost layer of the wall.† In other specimens only the spiral is evident. This mode of preservation, revealing a potential structure, is also found in the narrower tubes of zone *b* (fig. 117).

Certain oval or spherical thin-walled vesicles are met with at places in the regions between the brown tubes—one of them is seen below the tube in fig. 118. They suggest comparison with some of the fungal types already described, and in some cases have been observed to be borne on slender branched hyphæ. In the light of the common presence of such fungi in the portions of all the plants in this deposit, we are probably justified in regarding these vesicles as belonging to a saprophytic fungus, and not as a part of the structure of the organism under consideration. Their presence is noted, however, since in such an anomalous organism as *Nematophyton* they might prove to be of importance.

The small areas of different texture dotted through the inner region are frequently ill preserved and difficult to analyse. In fig. 116 they appear as dark masses owing to their greater opacity, the only structural feature that is indicated being the entrance of some of the wide tubes into the dark mass.

Careful examination of the best preserved examples shows that these wider tubes, which may have their rather thick wall preserved, resemble in cross-section the large tubes of the other specimen of *Nematophyton*. These wide tubes are accompanied by others of moderate fineness, and the bulk of the area seems to be made up of numerous still finer tubes closely entangled. The general resemblance in construction between these areas and the "medullary spots" in the other specimen is striking, and we have no doubt as to their being corresponding structures.

The region (figs. 113, 114, *b*) with the tubes arranged parallel to one another,

\* A similar mode of preservation was met with in *N. Hicksii* (cf. PENHALLOW, *loc. cit.*, 1889, p. 20).

† A very similar spiral marking, due to contraction and ridging of the inner layer of the cell-wall, is often met with in the cells of *Laminaria*. It has there been interpreted as an artefact due to drying or dehydration (cf. THODAY, Mrs M. G., *New Phytologist*, x (1911), p. 69).

and at right angles to the surface, shows similar elements to the inner zone differently arranged; the "medullary spots" are not, of course, represented. The vesicles and fine hyphæ mentioned above and regarded as a saprophytic fungus in connection with the inner zone, occur between the tubes of the outer zone also.

The tubes in the outer region are represented by their homogeneous brown contents, and can be traced from the irregularly running tubes of the inner region which bend outwards and branch. The free ends form the parallel tubes of the outer zone, which vary in thickness. They tend to widen slightly at their outer ends, where their tips stand at about the same level. Some of these tubes showed the same spiral marking as was described for the wider tubes of the inner tissue (fig. 117).

Between the vertically running tubes, and at places appearing to separate them into bundles, a granular mass is such a regular constituent of this outer zone as to suggest that it might have been based on a real structure, but the appearance is never decisive. When the clear evidence of breaking down and rearrangement afforded by the pseudo-cellular structure is taken into consideration, we are not prepared to attach significance to the brown granular masses in the outer zone, though attention may be directed to them.

The narrow, clear outer zone (figs 113, 114, *a*) above the summits of the vertical tubes is structureless, but the pseudo-cellular structure, that can be traced throughout much of the fragment, comes out very clearly here. It seems reasonable, in the light of the rest of the structure, to interpret this outermost zone as having been a structureless, and perhaps mucilaginous, layer during life. It has no sharply defined outer limit, though this is marked as a dark line owing to a granular deposit.

Although there is no continuity and the condition of decay or preservation is somewhat different, the second fragment described above has been treated as the peripheral region of *Nematophyton*. This peripheral region in previously known specimens of the genus has, at best, been represented by a thin coaly layer.\* The demonstration of the general structure of the peripheral region is the main addition to our knowledge of *Nematophyton* that is afforded by these specimens.

The affinities of *Nematophyton* with its remarkable and very consistent type of construction must still be regarded as an open question. The general opinion since CARRUTHERS' paper † has been that they were to be sought for in the Algæ, although there has always been difficulty in recognising a clear relationship to any algal group. There are difficulties in the way of a close comparison with *Laminariaceæ*, although in some respects the Rhynie specimens afford additional points

\* This layer is described as "very thin, hardly exceeding 3 mm." for *N. Loganii* (PENHALLOW, *Trans. Canad. Roy. Soc.*, vol. vi, 1888, p. 38), and as 1.5 mm. in *N. Ortonii* (PENHALLOW, *Ann. Bot.*, vol. x, 1896, p. 42).

† *Monthly Microscopical Journal*, vol. viii, 1872.

of comparison with this group. The wide non-septate tubes of *Nematophyton* have long been recognised as being more readily comparable with the tissues of such Algæ as the Udoteæ than with the septate cell-rows of the tissue derived by cell-division that make up the thallus of the *Laminariaceæ*,\* although the size attained by the fossil plant suggested comparisons with the latter.

While the general structure makes it somewhat difficult to think of *Nematophyton* as a land-plant, this possibility gains prominence in the light of the occurrence of the plant in the Rhynie deposit. DAWSON'S view of *Nematophyton Loganii* in the Lower Devonian rocks of Gaspé was that its large trunks had grown rooted in soils which were covered with a growth of *Psilophyton* and *Arthrostroma*, and that, while probably a marsh-plant, it was not marine.† The presence of *Nematophyton* in the terrestrial Rhynie deposit supports the conclusion drawn from the mode of occurrence of *N. Loganii* at Gaspé. Such a terrestrial mode of life of the plant would not be inconsistent with fragmentary remains being preserved in what are more probably marine deposits, while it is difficult to account for the repeated occurrence of a marine plant in terrestrial deposits. The facts so far known, although they involve difficulties, would thus appear to be in favour of *Nematophyton*, whatever its systematic position may prove to be, having been a marsh- or land-plant of Silurian and Devonian times.

*Nematophyton Taiti*, n.sp., Kidston and Lang.

Small fragment showing a construction of wide and narrow tubes characteristic of the genus. Tubes of wider system showing a range in size from 20  $\mu$  or less up to 52  $\mu$ ; mostly about 40  $\mu$ . Thickness of wall varying from 2  $\mu$  to 14  $\mu$  or more, probably in relation to condition of preservation. Some narrow tubes of this

\* It may be noted that a recent suggestion, while emphatically dismissing comparison with the *Laminariaceæ*, treats *Nematophyton* in connection with massive Fungi (CHURCH, *Thalassiophyta*, p. 49 and footnote).

† Dawson's views on this point are expressed in a number of his publications (e.g., *The Fossil Plants of the Devonian and Upper Silurian Formations of Canada*, 1871, and *The Geological History of Plants*, 1888), but most clearly and recently in PENHALLOW and DAWSON, *Trans. Canad. Roy. Soc.*, vol. vi, 1888, pp. 27-36. It will be remembered that these views were founded on study of the mode of occurrence of the plant as shown in the rock-sections exposed at Gaspé and the Bay des Chaleurs. Their nature may fairly be given by some extracts from the last-named paper, though the context should be consulted. "The mode of occurrence and state of preservation of the specimens seemed to make it certain that they had belonged to land-plants" (p. 27). "I also found stumps with branching roots apparently rooted *in situ* in the shales and argillaceous sandstones of the locality" (p. 28). "I also ascertained that these remarkable plants had probably grown in the clays and sands in which *Psilophyton* and other plants had been rooted, and consequently, that though probably marsh-plants they were not marine. They must have grown on low flats, probably often inundated, though whether this was with salt or fresh water is indicated merely by the negative fact that no properly marine organisms occur in the containing beds" (p. 28). "It was further found that *Psilophyton princeps*, *P. robustius*, *Arthrostroma gracile*, and *Cordaites angustifolia* were constant associates of these plants" (p. 29). In connection with the last quotation, it is to be noted that the remains referred to as *Cordaites angustifolia* were regarded by Dawson as of quite uncertain nature, and are even discussed as possible foliage of *Nematophyton* (*loc. cit.*, p. 34). Fig. 3 in the paper from which the above extracts have been made shows a trunk of *Nematophyton Loganii* resting on an underlay filled with *Psilophyton*. Fig. 4 shows another trunk embedded in a bed of shale containing *Psilophyton*, the bed being underlain and overlain by sandstone.

system can be traced into the medullary spots. These "spots" were about .2 to .3 mm. in diameter, and were originally occupied by narrow tubes about 10  $\mu$  in diameter.

Another fragment is regarded as the peripheral region of the plant. Internally it shows interlacing tubes and small medullary spots (.15 mm.). The tubes bend outwards, and in the superficial layer, which has a thickness of about 1 mm., stand parallel and at right angles to the surface. Externally there is a narrow amorphous layer above the free terminations of the tubes.

*Locality.*—Muir of Rhynie, Aberdeenshire.

*Horizon.*—Old Red Sandstone. (Not younger than the Middle Division of the Old Red Sandstone of Scotland.)

#### 5. THE SUCCESSION OF THE PLANTS AS SHOWN IN ONE COMPLETE VERTICAL SECTION OF THE BED.

The plant-containing chert was discovered by Dr MACKIE, as has been mentioned in previous papers, in the form of isolated blocks. The bed from which these came has since been successfully exposed by the Geological Survey. An account of the excavations made for this purpose is given in a Report\* of a Committee of the British Association. A set of blocks forming a complete vertical section from Trench No. 1 has been available for our investigation, and a general account of this section was included in Part I of this series of papers. Since then thin sections for microscopical examination of all the plant-containing beds of this vertical section have been studied. We are thus able to extend and qualify our earlier account, and to indicate more precisely the distribution of the plants throughout the chert-band at this one spot, where it was about eight feet in thickness.

In the following description the numbering and lettering of the beds † as given in the section represented on pp. 762-3 of Part I will be adhered to, and the composition of the beds followed from below upwards. While the description will be based on the actual section in one vertical plane, variations in the succession of the plants, especially in the critical lower region of the bed, must be taken into consideration. The information afforded by certain loose blocks referable to this region can suitably be included in the description.

Above the bed of clay passing down into bedded shales the eight-foot section of

\* *Brit. Assoc. Rep.*, 1916 (Newcastle), p. 206.

† The following slides in the Kidston Collection give a complete survey of this vertical section:—

N 20, 2561	K 15, 2562	E 10, 2566
N 19, 2429	I 14, 2435	E 9, 2518
M 18a, 2560	H 13, 2563	D 8, 2543
M 18b, 2559	G 12, 2564	B 6, 2449, 2567, 2458, 2487
L 17, 2558	F 11a, 2565	A <sup>2</sup> , 2499
L 16, 2430	F 11b, 2556	A <sup>1</sup> , 2492, 2447, 2444, 2533, 2514, 2423.

When a number of slides are mentioned, as in B 6 and A<sup>1</sup>, they are in descending order through the bed.

the chert-band in Trench No. 1 commences with the bed marked A". This bottom region of the chert is of special interest, since all the species of vascular plants and practically all the types of Thallophyta found in the deposit have been met with in its thickness of 1 foot 3 inches, and indeed in the lower portion Bed A"1. The basal region consists of a pure accumulation of *Rhynia Gwynne-Vaughani*, usually in a clear peaty matrix. Occasionally sporangia of *R. major* have been met with in the peat thus formed. Above this came a peat formed of more or less decayed *Hornea Lignieri*, rhizomes, stems, and sporangia of this plant being present. In the upper portion of this region *Rhynia major* is associated with the *Hornea* (Part III, fig. 2). Overlying this *Hornea* peat came a sandy bed enclosing remains of *Asteroxylon* and some *Hornea*. The *Asteroxylon* was best preserved immediately above the *Hornea* peat, and its rhizomes extended down into the latter, penetrating portions of the plants (Part III, fig. 2; Part IV, fig. 24). On passing further upwards into the dark sandy Bed A"2 the preservation of the stems of *Asteroxylon* embedded in the sandy matrix is less good.

While this is the succession shown in one block at this particular spot, other blocks known to have come from the same level at no great distance show that it was not invariable. Thus in one block a clear peaty matrix with stems and sporangia of *Hornea* mixed with rhizomes, stems, and intermediate regions of *Asteroxylon* came in place of the pure *Hornea* peat. Another block had the typical *Rhynia Gwynne-Vaughani* peat below, and above this well-preserved *Asteroxylon* in a clear peaty matrix. A very similar block had the *Rhynia Gwynne-Vaughani* peat below followed by a zone with *Asteroxylon* only, while another thin layer of *Rhynia Gwynne-Vaughani* came above this. With the exception of this last specimen, peat composed of *R. Gwynne-Vaughani* has only been seen at the extreme base of this bed. It was not met with above Bed A"1 in the section studied.

In view of the limitation of *R. Gwynne-Vaughani* to the base of the section of the bed as exposed *in situ*, it is convenient to refer in this place to two loose blocks of particular interest. One of these is the cubical block, from the weathered face of which fig. 2 in Part I was taken. This block, which is now in the Natural History (British) Museum, proves that at some places in the bed there was an accumulation of pure *R. Gwynne-Vaughani* peat to a depth of at least 12 inches. The other is the block represented in Part I, fig. 5, in which the closely associated, tapering stems of *R. Gwynne-Vaughani* stood practically erect, as they had grown above a peat composed of the remains of the same plant.

Returning to the description of the section from Trench I, it is to be noted that following on Bed A"2 came a definite band of cherty sandstone of some thickness (A"3, A'). This had streaks of carbonaceous matter, but, owing to the absence of plant-remains showing structure, it was not studied in detail.

The thick Bed B 6 again exhibits peaty structure, being composed throughout of plant-remains with their form and structure fairly well preserved. These lay in a

peaty matrix interrupted by irregular sandy layers. One block including the whole thickness of this bed was divided into four by horizontal planes, and the distribution of the plants followed in vertical sections of the four portions. The peat of the lowest quarter of the bed contrasts sharply with the underlying sandy band in the absence of inorganic constituents. It has a peaty matrix with spores and fragments of plant-tissues and, embedded in this, fairly well-preserved rhizomes, stems, and sporangia of *Hornea*. The sections studied show a practically pure *Hornea* peat with a very occasional stem that may belong to *Rhynia*. The division of Bed B above this shows a sandy matrix enclosing remains of *Hornea* and *Asteroxylon*, and overlying this a *Hornea* peat similar to that just described. The succeeding region has the peat much interrupted and mixed with sand; the plant-remains are *Hornea* and *Asteroxylon*. The uppermost region of B 6 shows the same mixture of peat and sand; the plants are *Hornea*, *Asteroxylon*, and *Rhynia major*.

It is characteristic of Bed B 6, in contrast to A<sup>1</sup>, that the peat is more interrupted by irregular sandy layers. The preservation of the plant-remains also is different, their tissues tending to become amorphous and yellow. The indications of accumulation of the peat by growth *in situ* of the vascular plants are less definite than in the case of the beds below; the appearances are equally consistent with the view that the plant-remains might have been carried a short distance from adjacent growths of the plants.

Above Bed B 6 came the second definite bed of fine siliceous sandstone (C); this was not examined in detail, owing to the obvious absence of plant-remains.

The succeeding three and a half feet of the chert-bed in the section from Trench No. 1 contained, so far as we have observed, only *Rhynia major*. The main peaty beds are separated by sandy layers, and similar more irregular bands of dark sandy matrix interrupt the thicker masses of peat. This composition is well illustrated by the block from Bed E 10 that was represented natural size in Part I, fig. 1.\*

The condition of preservation of the remains of *Rhynia major* may be noted very briefly, taking the beds in order. In Bed D the peaty mass is yellow and almost amorphous, only a few of the stems showing recognisable structure. In contrast to this type of preservation the stems in Bed E, which are often of large size, retain their cellular structure, although they may be more or less decayed and broken down. Rhizomes of *Rhynia major* have been found in this bed. In the lower portion of the following bed (F 11*b*) the peat is composed of greatly altered plant-remains, which are shown to be *Rhynia major* by a few recognisable stems; the general condition of this bed is similar to that of Bed D. An isolated tracheide of *Asteroxylon* was found in the matrix. In the upper portion (F 11*a*) the stems in various conditions of decay retain the cellular structure in the more usual way; some resemble rhizomes, although rhizoids have not been seen. Beds G 12 and H 13 contained more or less decayed stems of *R. major*, sometimes associated with

\* This block of the chert is preserved in the British Museum (Natural History).

sporangia. The stems in Bed I 14, though somewhat decayed, are hardly compressed and lie loosely in the peaty matrix which separates them. The smaller stems have a stellate outline, due to unequal contraction with ridging of the surface; they were evidently less firm and rigid in life than the larger stems. The section of Bed K shows that the lower portion consists mainly of peaty and sandy matrix, above which comes a narrow layer of peat with uncompressed stems that are almost amorphous. In the lower (L 16) and upper (L 17) portions of the following Bed L, which still contains *Rhynia major* only, the preservation of the tissues is of the usual type. Very well-preserved stems, which may even show the contracted protoplasmic utricles of the cells, occur alongside others that are more or less decayed or broken down. In Bed M a change in the composition of the peat is met with. Stems of *Rhynia major* are found as in the preceding beds; mixed with these in M 18*b* and throughout the upper portion (M 18*a*) forming a pure peat, there are remains of *Hornea*—stems, rhizomes, and sporangia being present. *Hornea* having thus reappeared in this section of the chert-band, persists in the two levels of the last peat-bed N. In N 19 the prominent remains are large and very perfectly preserved stems of *Rhynia major*, but stems and sporangia of *Hornea* are associated with them. In N 20, the uppermost bed of the chert-band showing a peat formed of plant-remains, this is composed entirely of the parts of *Hornea* with their usual rather imperfect preservation. The last bed of the section, marked O, which consisted of siliceous sandstone with carbonaceous remains, was not examined in detail.

Having thus traced the vertical distribution of the vascular plants through this section of the deposit, the general distribution of the Thallophyta remains to be indicated. This need not be treated in detail, for there is evidence that some forms of fungi are present in the lowest and highest beds. Their nature and abundance in the various beds show a general relation to the remains of vascular plants composing the peat and their mode of preservation. Practically all the Thallophyta that have been described occurred in Bed A''1 at the base of the deposit; it has been shown above that all the vascular plants were present in this region also. Some of the fungi have only been found in this lower region (e.g. *Palæomyces Asteroxyli*, *P. Hornæ*). Others, such as *P. agglomerata* and the intrusive fungus described as Fungus No. 14, occurred here and are met with again in the *Hornea* peat of the uppermost beds. The most widely distributed fungus was *Palæomyces Gordoni*, often with intrusive forms of the types described under Fungus No. 15.

Of other Thallophyta, unicellular Bacteria were probably widespread, but, for reasons that have been given, are difficult to identify. The filamentous form described as Schizophyta No. 2 (*Archæothrix contexta*) was typically present as a felt above the *Rhynia Gwynne-Vaughani* peat at certain places in Bed A''1. It also occurred around decaying fragments of *R. Gwynne-Vaughani*, and is met with again in Bed

F 11b. It is of interest, as indicating a recurrence of similar, probably submerged, conditions at these levels, that the algal remains described under the name *Algites Cranii* occur at the same two levels in the chert-band.

The fragments of *Nematophyton* have only been met with at one spot in the clear peaty matrix of Bed A''1, some little distance above the level where the felt of Schizophyta No. 2 and the remains of *Algites Cranii* occurred.

It is noteworthy that Crustacean remains were most abundant in the *Rhynia Gwynne-Vaughani* peat of the lower region of Bed A''1, where the last-named plants were found.

#### 6. REMARKS ON THE NATURE, CONDITIONS OF ACCUMULATION, AND PRESERVATION OF THE RHYNIE DEPOSIT.

In the first of this series of Memoirs (Part I, p. 764) some remarks were made and a general view expressed regarding the nature and origin of the silicified chert-band found at Rhyrie. The accumulation of beds rich in plant-remains and free from admixture of mineral particles was compared to the growth of a modern peat. The fact that the peat is interrupted at intervals by more or less regular sandy layers was interpreted as indicating frequent flooding of the surface. The silicification was regarded as due to a final saturation of the peat-bed, or rather the system of peat-beds and sandy layers, by water with silica in solution, derived from fumaroles or geysers.

As a general hypothesis which covers the main facts this may stand. Now that the plant-remains have been examined throughout a complete vertical section, it is possible, however, to amend and amplify this view in some points of detail.

The outstanding features of the Rhyrie bed as shown in the section described above may, in the first place, be summarised, since it is from a consideration of them that any more detailed indications as to the conditions of accumulation of the deposit can be expected. It has been seen that—

(a) The structural characters of *Rhynia* and *Asteroxylon*, especially the presence of stomata in the epidermis from the base of the stem upwards, indicate that the growth of these plants was not truly aquatic. The soil may, of course, have been swampy or saturated with water. On the other hand, *Hornea* might have grown in shallow water, though there is no direct evidence for this.

(b) There are indications of growth *in situ* of *Rhynia Gwynne-Vaughani* in the basal bed, of *Asteroxylon* in the sandy layer covering the *Hornea* peat of Bed A''1, and of the *Hornea* in the same region. There is also evidence for the growth *in situ* of *Rhynia major* in the peat of some of the upper beds. These various indications justify us in regarding the peat-layers as largely formed by the growth of plants on the spot; the carriage of remains from the near neighbourhood and their accumulation, possibly under water, is not excluded in the case of some of the beds.

(c) *Rhynia Gwynne-Vaughani* has only been met with at, and slightly above, the base of Bed A"1, i.e. at the extreme base of the deposit. *Asteroxylon*, except for an isolated tracheide in Bed F 11b, has not been met with above Bed B 6. *Hornea* occurs in the lower beds up to Bed B 6, and reappears in the uppermost Beds M and N. *Rhynia major* is only an occasional and relatively unimportant component of the beds up to B 6. Above this from D to L it forms the whole deposit, being then gradually replaced by *Hornea* in the uppermost beds.

(d) The change in composition of the plant-remains above the *Rhynia Gwynne-Vaughani* zone at the base takes place without any intervening sandy layer. The succeeding peat may be composed of *Hornea* with some *Rhynia major*, but this in other blocks is represented by loosely packed *Hornea* and *Asteroxylon*, or by *Asteroxylon* only.

(e) The peat-beds are separated and interrupted by sandy layers of two sorts: (1) There is a very definite bed of sandstone separating the characteristic remains of A"1 and A"2 from the different type of peaty deposit in B 6. Another definite sandstone layer occurred at C, and was followed by the succession of beds with pure *Rhynia major*. (2) The separation of the other peat-beds is due to an accumulation of sand mixed with abundant plant-remains, the decay of which has been more or less complete. The passage of the plant-remains into thin carbonaceous partings can be followed at places. The less marked interruption of the peat-beds is due to similar irregular accumulations of sand and, associated with this, more complete decay of the vegetable tissues. Occasional isolated grains of sand in the peat itself indicate the other extreme of the association of sand with the peaty mass.

(f) There are indications in the different nature of the preservation of the stems and from associated algal remains of more aquatic conditions at certain levels. This can be regarded as probable for the region above *Rhynia Gwynne-Vaughani* in A"1, and for Beds D and F 11b. Possibly the presence of *Hornea* is another indication of moister conditions: in connection with this the reappearance of this plant in Beds M and N is to be noted.

(g) The loose packing and excellent preservation of the plant-remains in the basal beds is a remarkable feature of the deposit. There is no regular increase in decay and compression on passing from the upper peat-beds downwards.

Certainty as to the exact conditions of accumulation of this ancient deposit is probably unattainable. Our knowledge of the details of accumulation of various deposits at the present day, which might afford further help, is only sufficient to serve for the institution of general comparisons. A consideration of the facts summarised above with some others appears, however, to justify a further interpretation of the story to which the following remarks are a contribution.

The more detailed examination of the peat-like bands themselves has supported the interpretation of their nature which is expressed in the term "silicified peat" used throughout these papers. In some cases it is clear that the plants grew in the

position in which their remains are found; it is possible, though not certain, that in other cases the remains may have accumulated in water from plants growing close by. The structure of the resulting mass, excluding the sandy bands, agrees with that of recent peats in the absence of mineral particles and the presence of a matrix embedding more or less well-preserved portions of plants. The matrix, though in great part amorphous, must have had sufficient consistency to support the fragments of tissues, spores, etc., evenly distributed through it. The decay of the plant-remains is to be associated with the presence of saprophytic fungi in them, and doubtless also with the action of bacteria. It seems to have taken various forms and to have been arrested at various stages. The arrest may have been related to absence of oxygen; the more thorough decay in relation to the admixture of sand supports this view. Hyphæ and resting-spores of fungi are chiefly found in relation to the plant-remains, and when they occur in the matrix were probably in great part, though not entirely, set free by the decay of the plants.

All these features find close parallels in recent peats, especially when the structure of the latter is examined in microscopical sections. The component plants are, of course, quite different, and the fungi do not belong to the same types. Persistent dark hyphæ and resting-spores and sclerotia occur abundantly in the plant-remains and the amorphous matrix of recent peats. Recent peats, however, become more amorphous on passing downwards, and the difference in this respect of the Rhynie deposit will require to be considered below.

The presence of numerous layers of sand interrupting the peat in the Rhynie deposit is a feature in which it differs from most recent peats. We have no definite evidence showing that this sand was wind-borne, and therefore suggested frequent inundations to account for the irregular layers of sand, and more prolonged submergence to account for the more definite sandstone beds. The possibility of some of the sand having been wind-borne must, however, be kept in mind. This applies especially to the irregular sandy layers and the scattered grains in the matrix of the peat. The dark colour of these regions appears to be due to the altered vegetable matter; decomposition seems to have been complete and rapid in the sandy layers. The vegetable remains thus represented in the layers of sandy matrix must correspond to a considerable thickness of the peat, any remains of stems, etc., that persist being almost completely flattened.

Since the Rhynie deposit occurred in what is known to have been an actively volcanic region, it is reasonable to regard the silicification of the bed as in some way due to water containing silica in solution, possibly derived from fumaroles. The separation of silica in the colloidal form may have been determined, in part at least, by the decaying plant-remains. Such a deposition of silica is known to follow from the growth of Cyanophyceæ and Bacteria, and around decaying organic material in hot springs. The Rhynie chert may have been the result of a somewhat similar process.

When we take into consideration the composition of the water of siliceous springs at the present day, it further seems quite possible that plants like *Rhynia* may have grown in a substratum saturated with the siliceous solution. In the light of what is known as to the vegetation found around siliceous springs at the present day, the xerophytic construction of the Rhynie plants may be of significance. In the case of the vegetation around fumaroles in Java\* the plants are xerophytic, rooted in the hot acid soil, and with their foliage exposed to hot sulphurous vapours. The soil consists of a white siliceous clay. The clay underlying the Rhynie deposit might possibly be regarded as of this nature, while corresponding in its effects on the vegetable remains above to the clay beneath recent peats.

The possibility that the water saturating the Rhynie plant-remains might have been siliceous throughout their accumulation may further explain a most striking difference between the preservation of this bed, considered as a whole, from what is found in recent peats. In the case of the latter the best preservation is met with in the upper region, decay and compression being marked in the lower part of the bed. In the Rhynie deposit, on the other hand, the preservation is as good in the lowest beds of the eight-foot section as it is above. Further, the plant-remains at the base of the deposit are not compressed, and are often loosely placed in the matrix. It was suggested above that the water around the growing plants might have been siliceous, and that the decay going on in the accumulating remains might have determined the separation of colloidal silica; there are indications from the microscopic sections that this separation did occur round the plants in the matrix in the first instance. On this view the silicification, or at least its early stages, would have been progressive as the bed was accumulating, instead of the thick peat-bed being first formed and then at a later date silicified as a whole. Such an explanation would account for the loose packing and perfect preservation of the plants in the basal beds where, on the analogy of recent peats, the greatest alteration and decay would have been anticipated.

The peculiar changes which are involved in the development of hemispherical projections in *Rhynia Gwynne-Vaughani* and the necrosis areas, wound-reactions and unequal enlargement of cells in the stems of this species and of *R. major* (see Part IV, pp. 835-6), must be recalled here. These various developments suggested a reaction to some prolonged external stimulus. The possibility that this was connected with the volcanic conditions that accompanied the supply of the siliceous water appears to be a justifiable speculation to raise. The intumescences and other reactions that are known to follow on the stimulus of irritating vapours in the case of existing plants (Part IV, p. 834) should be borne in mind in considering this.

The characters of the deposit as a whole appear to indicate a steady growth and accumulation on a subsiding surface. This might have been a swamp beside

\* Cf. SCHIMPER, *Plant Geography*, p. 386, and literature there cited.

a stream or the edge of a small lake or pond, perhaps fed by the water from a fumarole or siliceous spring. There appears to have been a primary vegetation of *Rhynia Gwynne-Vaughani* over the moist clayey surface. This led at places to a growth of peat formed *in situ* from the perished remains of this plant. Occasional sporangia from plants of *Rhynia major* growing in the neighbourhood fell into the peat as it formed. In the region represented by the main section of the bed, this primary covering of *Rhynia Gwynne-Vaughani* was arrested, never to recur, by the subsidence bringing water, probably charged with silica, over the surface. The necroses and associated wound-reactions are especially marked at this level. The abundance of remains of the small Crustacea and the presence of *Algites Cranii* appear to further indicate the more aquatic conditions that supervened. It seems probable that this provided the suitable environment for *Hornea*, the remains of which were accumulated *in situ* as the *Hornea* peat of A"1. *Asteroxylon* appears to have occurred *in situ* with its rhizomes penetrating this *Hornea* peat as drier conditions recurred. Then followed the first definite sandstone band, perhaps marking a further period of subsidence and sedimentation. This is consistent with the presence of *Hornea* (mixed with the remains of *Asteroxylon*) throughout Bed B 6, and the deposition of another definite sandstone layer above this. From this period onwards the growth of *Rhynia major* appears to have kept pace with the subsidence, thus leading to the accumulation of a thick mass of peat. The sandy layers interrupting this may indicate either floodings or accumulations of blown sand—perhaps both. There are occasional indications of more aquatic conditions in the course of the accumulation of this mass of *Rhynia major* peat. Finally the subsidence seems to have been more active and more aquatic conditions returned, bringing in *Hornea*, which replaced *Rhynia major*. With increasing depth, sediments without plant-remains were deposited over the peat-bed.

While this interpretation of the changes of conditions indicated by the section of the peat-bed studied is speculative, and it would be dangerous to press the comparisons into detail, some such way of looking at the facts seems justified. It enables us to comprehend the mode of accumulation of the deposit in a gradually subsiding marsh or small lake in much the same way as such regions get filled up with peat at the present day. The differences from modern peats, as well as the resemblances, must of course be borne in mind.

The interesting and puzzling fact of the occurrence of fragments of *Nematophyton* in the deposit has been regarded above as supporting the view that this anomalous plant grew on land. How the fragments got into the peat, and what is the geological and botanical interest of their presence, must remain to some extent open questions pending further knowledge of this remarkable plant and of the Rhynie deposit as a whole.

The accumulation of vascular plants in the Rhynie chert-band was clearly derived from a continued growth on a land-surface that was at times submerged.

The abundance of fungi and the presence of an alga suggesting comparison with Characeæ are consistent with this. No evidence of marine conditions has been met with in the study of the plant-remains. The plant-containing chert discovered at Rhynie thus provides a special, but quite definite, record of a land surface covered with vegetation in the Early Old Red Sandstone of Scotland.

## EXPLANATION OF PLATES.

(All the figures are from untouched photographs.)

## PLATE I.

*Fungus No. 1.*

Fig. 1. A strand of stout septate hyphæ from a longitudinal section of a partially decayed stem of *Asteroxyylon*.  $\times 100$ . (No. 2521.)

Fig. 2. Strand of hyphæ from the same stem with only very occasional septa; at places the branched hyphæ form irregular knots.  $\times 100$ . (No. 2521.)

Fig. 3. Septate hyphæ from the strand in fig. 1.  $\times 250$ . (No. 2521.)

Fig. 4. Non-septate hyphæ from the strand in fig. 2.  $\times 250$ . (No. 2521.)

*Fungus No. 2. (Palæomyces Gordoni.)*

Fig. 5. Portion of a longitudinal section of a stem of *Asteroxyylon*. The soft tissues (phloem) of the stele are replaced by strands of stout, longitudinally running hyphæ similar to those in the preceding figures. In the adjacent cortex are three large resting-spores of Fungus No. 2.  $\times 34$ . (No. 2494.)

Fig. 6. Portion of a longitudinal tangential section of a partially decayed stem of *Asteroxyylon* showing hyphæ and resting-spores of Fungus No. 2 in the middle cortex.  $\times 50$ . (No. 2522.)

Fig. 7. Portion of same section as fig. 6.  $\times 100$ . (No. 2522.)

Fig. 8. Some of the finer hyphæ and collapsed vesicles in the same section.  $\times 250$ . (No. 2522.)

Fig. 9. Single resting-spore of Fungus No. 2 borne on a stout lateral branch of a more slender hypha.  $\times 250$ . (No. 2522.)

Fig. 10. Mature resting-spore of Fungus No. 2 showing the double contour due to the inner layer of the wall having separated from the outer layer.  $\times 250$ . (No. 2522.)

Fig. 11. Another resting-spore showing fine threads of wall substance between the outer and inner layers of the wall.  $\times 210$ . (No. 2522.)

## PLATE II.

*Fungus No. 3. (Palæomyces Gordoni var. major.)*

Fig. 12. Large thick-walled resting-spores of Fungus No. 3 with, to the right, a resting-spore intermediate in size between this and the spores of Fungus No. 2.  $\times 100$ . (No. 2527.)

Fig. 13. Another specimen showing the stout hyphal stalk on which the resting-spore is borne.  $\times 100$ . (No. 2479.)

Fig. 14. Portion of the wall of the resting-spore of Fungus No. 3 showing an outer layer, a broad middle layer, and an inner layer; within the latter a thin layer bounding the contents is contracted away.  $\times 250$ . (No. 2527.)

*Fungus No. 4.*

Fig. 15. Group of resting-spores of Fungus No. 4 from a decayed stem of *Asterozylon*.  $\times 100$ . (No. 2528.)

Fig. 16. Three of the resting-spores from fig. 15.  $\times 250$ . (No. 2528.)

*Fungus No. 5.*

Fig. 17. Small, oval, thick-walled resting-spores of Fungus No. 5 from a decayed stem of *Rhynia major*.  $\times 100$ . (No. 2529.)

Fig. 18. Some of the resting-spores from fig. 17.  $\times 250$ . (No. 2529.)

*Fungus No. 6.*

Fig. 19. Hyphae bearing oval and spherical vesicles from a partially decayed stem of *Rhynia major*.  $\times 250$ . (No. 2393.)

*Fungus No. 7. (Palæomyces Asterozyli.)*

Fig. 20. Hyphae of various diameters and vesicles of Fungus No. 7 from the decayed inner cortex of a rhizome of *Asterozylon*.  $\times 100$ . (No. 2439.)

Fig. 21. Stout hyphae of Fungus No. 7, one of which is branching.  $\times 250$ . (No. 2525.)

Fig. 22. Two longitudinally running hyphae of Fungus No. 7, showing a transverse, anastomosing branch.  $\times 250$ . (No. 2525.)

Fig. 23. Fine hyphae of Fungus No. 7 dilating into oval vesicles.  $\times 250$ . (No. 2530.)

Fig. 24. Fine hypha of Fungus No. 7 dilating into a vesicle.  $\times 250$ . (No. 2439.)

PLATE III.

Fig. 25. Longitudinal section of outer portion of a rhizome of *Asterozylon* showing the two layers of outer cortex practically free from the fungus, the hyphae and vesicles of which are present between the cells of the inner cortex.  $\times 100$ . (No. 2525.)

Fig. 26. Portion of tangential section of the inner cortex of another rhizome of *Asterozylon* showing the intercellular position of the fungus.  $\times 100$ . (No. 2468.)

Fig. 27. More broken-down portion of inner cortex of a rhizome showing the hyphae and vesicles of Fungus No. 7.  $\times 100$ . (No. 2530.)

Fig. 28. Two cells of the outer cortex of the rhizome of *Asterozylon* shown in fig. 25. The figure shows hyphae on the surface of the cortex with, to the left, a recurved, hook-like branch (*a*); on the right the fungus with a vesicle (*b*) appears to be within a superficial cell.  $\times 250$ . (No. 2525.)

*Fungus No. 8. (Palæomyces Hornea.)*

Fig. 29. Portion of a section of the rhizome of *Hornea* showing hyphae and resting-spores of Fungus No. 8 between the cells of the tissue.  $\times 100$ . (No. 2531.)

Fig. 30. Outer portion of a rhizome of *Hornea* showing strands of stout hyphae and a hyphal tangle.  $\times 75$ . (No. 2531.)

Fig. 31. Vertical section of another rhizome of *Hornea* showing a hypha entering from the hyphal mass outside and ramifying between the cells of the rhizome.  $\times 75$ . (No. 2532.)

Fig. 32. Hypha of Fungus No. 8 between cells of rhizome.  $\times 250$ . (No. 2531.)

Fig. 33. Portion of the hyphal knot shown in fig. 30.  $\times 250$ . (No. 2531.)

Fig. 34. Resting-spore and hyphae of Fungus No. 8 in rhizome of *Hornea*.  $\times 250$ . (No. 2531.)

Fig. 35. Group of mature resting-spores, presumably of Fungus No. 8, in relation to decayed rhizomes and stem-bases of *Hornea*.  $\times 100$ . (No. 2443.)

PLATE IV.

*Fungus No. 9. (Palæomyces vestita.)*

Fig. 36. Longitudinal section of the cortex of the stem of *Asteroxylon* showing the resting-spores of Fungus No. 9 distributed through the decayed tissues, and also within a large resting-spore of Fungus No. 2.  $\times 100$ . (No. 2454.)

Fig. 37. Resting-spores of Fungus No. 9 showing their investment by fine hyphæ.  $\times 250$ . (No. 2473.)

Fig. 38. Hyphæ and resting-spores of Fungus No. 9; some of the latter are invested by the fine hyphæ.  $\times 250$ . (No. 2454.)

*Fungus No. 10. (Palæomyces agglomerata.)*

Fig. 39. Group of hyphæ and resting-spores of Fungus No. 10 in relation to a decayed stem of *Rhynia Gwynne-Vaughani*.  $\times 100$ . (No. 2533.)

Fig. 40. Portion of group in fig. 39 showing hyphæ and spores.  $\times 250$ . (No. 2533.)

Fig. 41. Portion of group in fig. 39. Intercalary enlargements to form spores are seen in some hyphæ.  $\times 250$ . (No. 2533.)

*Fungus No. 11.*

Fig. 42. Hyphæ and small vesicles of Fungus No. 11 breaking out from a tissue cell of *Rhynia Gwynne-Vaughani*.  $\times 250$ . (No. 2534.)

Fig. 43. Hyphæ and small vesicles of Fungus No. 11 in the position of the dark layer of cells below the outer cortex of a decayed stem of *Rhynia Gwynne-Vaughani*.  $\times 500$ . (No. 2527.)

*Fungus No. 12.*

Fig. 44. Cortex of *Rhynia Gwynne-Vaughani* containing hyphæ and vesicles of Fungus No. 12.  $\times 100$ . (No. 2535.)

*Fungus No. 13. (Palæomyces Simpsoni.)*

Fig. 45. Surface of a decayed stem of *Rhynia Gwynne-Vaughani* in a section from Mr SIMPSON, showing an oval break in the surface beneath which are the crowded young vesicles of Fungus No. 13.  $\times 100$ . (No. 2568.)

Fig. 46. Group of stalked vesicles of Fungus No. 13 projecting from the surface of the same stem.  $\times 100$ . (No. 2568.)

Fig. 47. Some of the vesicles in fig. 46.  $\times 250$ . (No. 2568.)

PLATE V.

*Fungus No. 14.*

Fig. 48. Globular mass of fine hyphæ and resting-spores and short stalk composed of associated fine hyphæ of Fungus No. 14.  $\times 100$ . (No. 2533.)

Fig. 49. Resting-spores from specimen in fig. 48.  $\times 250$ . (No. 2533.)

Fig. 50. Mass of hyphæ and resting-spores of Fungus No. 14 enclosed by the thick wall of the resting spore of Fungus No. 3.  $\times 100$ . (No. 2536.)

Fig. 51. Fine hyphæ of Fungus No. 14 filling the cavity of a partially decayed resting-spore of Fungus No. 3 and its hyphal stalk.  $\times 100$ . (No. 2479.)

Fig. 52. Resting-spore of Fungus No. 3 with groups of vesicles and hyphæ of Fungus No. 14 on the surface.  $\times 100$ . (No. 2537.)

Fig. 53. Same specimen seen from other side in section.  $\times 100$ . (No. 2537.)

Fig. 54. Another specimen from Fungus No. 3 showing vesicles and hyphæ of Fungus No. 14 on the surface.  $\times 100$ . (No. 2428.)

Fig. 55. Medium-sized, thick-walled, resting-spore of Fungus No. 3 containing the resting-spores formed on hyphae of the intrusive Fungus No. 14.  $\times 100$ . (No. 2443.)

Fig. 56. Spores within the thick boundary wall from the preceding figure.  $\times 250$ . (No. 2443.)

*Fungus No. 15.*

Fig. 57. Group of thick-walled resting-spores of Fungus No. 2; two of these contain the intrusive Fungus No. 15.  $\times 100$ . (No. 2538.)

Fig. 58. One of the resting-spores in fig. 57 showing the spores of the intrusive Fungus No. 15.  $\times 250$ . (No. 2538.)

PLATE VI.

Fig. 59. Resting-spore of Fungus No. 2 containing small spores of Fungus No. 15 within the main cavity and also between the layers of the wall.  $\times 100$ . (No. 2539.)

Fig. 60. Large resting-spore containing spores of the intrusive Fungus No. 15.  $\times 250$ . (No. 2432.)

Fig. 61. Resting-spore of Fungus No. 2 containing well-preserved spores of the intrusive Fungus No. 15.  $\times 100$ . (No. 2427.)

Fig. 62. Spores from the specimen in fig. 61.  $\times 250$ . (No. 2427.)

Fig. 63. Group of resting-spores of Fungus No. 2, two of which contain the intrusive Fungus No. 15.  $\times 100$ . (No. 2427.)

Figs. 64 and 65. Two of the specimens in fig. 63 more highly magnified to show the remains of fine hyphae attached to the spores of the intrusive fungus.  $\times 250$ . (No. 2427.)

Fig. 66. Spores of an intrusive fungus from another large resting-spore showing remains of the fine hyphae.  $\times 500$ . (No. 2540.)

Fig. 67. Resting-spore of Fungus No. 2 enclosing large thin-walled resting-spores of an intrusive fungus, some of which in turn are occupied by a smaller fungus.  $\times 250$ . (No. 2435.)

Fig. 68. One of the enclosed spores from fig. 67 showing the smaller spores and stalk-like remains of hyphae within it.  $\times 500$ . (No. 2435.)

Fig. 69. Resting-spore of Fungus No. 2, packed with spores of the intrusive fungus, which at one point have burst through the wall.  $\times 100$ . (No. 2541.)

Fig. 70. Portion of the preceding specimen showing the hyphae and vesicles bursting the enclosing wall.  $\times 250$ . (No. 2541.)

Fig. 71. Resting spore of Fungus No. 2 with the thin-walled spores of the intrusive fungus on its exterior.  $\times 225$ . (No. 2542.)

*Fungi not sorted into Form-types.*

Fig. 72. Spherical spores distributed through a decayed stem of *Rhynia Gwynne-Vaughani*.  $\times 100$ . (No. 2391.)

Fig. 73. Two of these spores.  $\times 250$ . (No. 2391.)

PLATE VII.

Fig. 74. Small fungal spores distributed through a decayed stem of *Rhynia Gwynne-Vaughani*. A large thin-walled spore (*cf.* fig. 76) is present with them.  $\times 100$ . (No. 2543.)

Fig. 75. Some of the small spores in the preceding figure.  $\times 250$ . (No. 2543.)

Fig. 76. One of the large thin-walled spores accompanying the small spores (*cf.* fig. 74) containing four well-defined spores.  $\times 250$ . (No. 2543.)

Fig. 77. Small spores(?), possibly fungal, but with appearances suggesting algal cells.  $\times 500$ . (No. 2544.)

Fig. 78. The same.  $\times 1000$ . (No. 2544.)

Fig. 79. Two spherical groups or colonies of dark cells of uncertain nature.  $\times 100$ . (No. 2558.)

Figs. 80A, 80B. Two views of a resting-spore of a fungus with a peculiar covering of delicate radiating tubes.  $\times 500$ . (No. 2545.)

Fig. 81. Well-preserved fungal resting-spores borne on hyphæ free in the matrix.  $\times 210$ . (No. 2555.)

Fig. 82. Portion of peripheral region of a stem of *Rhynia major*. *ep.*, epidermis; *o.c.*, outer cortex; *x.*, layer of cells with problematical dark contents; *i.c.*, inner cortex.  $\times 100$ . (No. 2407.)

Figs. 83, 84. Cells of the layer with problematical dark contents in the preceding figure, showing some indications of fine hyphal nature of the contents.  $\times 250$ . (No. 2407.)

#### *Schizophyta.*

Fig. 85. Colonial masses of unicellular bacteria from matrix of the peat.  $\times 100$ . (No. 2546.)

Fig. 86. Colonies of a recent bacterium, unstained, for comparison with fig. 85.  $\times 100$ .

#### PLATE VIII.

Fig. 87. Portion of the peaty matrix showing the felted arrangement of the fine filaments of a possible filamentous bacterium. (Schizophyta No. 2.)  $\times 100$ . (No. 2479.)

Fig. 88. Portion of arrangement specimen.  $\times 250$ . (No. 2479.)

Fig. 89. General arrangement of two groups of *Archæothrix oscillatoriformis* in a cavity of a stem of *Rhynia Gwynne-Vaughani*.  $\times 100$ . (No. 2542.)

Fig. 90. Single filament of *Archæothrix oscillatoriformis* from the preceding figure, showing the small, discoid cells.  $\times 650$ . (No. 2542.)

Specimens received from Rev. Mr CRAN, placed with *Algites (Palæontitella) Cranii*.

Figs. 91, 92. Views at two depths of focus of a small verticillately branched axis.  $\times 100$ . (No. 2570.)

Fig. 93. Portion of same specimen showing three nodes with the whorled appendages.  $\times 150$ . (No. 2570.)

Fig. 94. Transverse section of a node showing corticating cells and whorled appendages.  $\times 200$ . (No. 2569.)

Fig. 95. Tubular rhizoid (?) with cellular node and two swollen cells borne at this.  $\times 100$ . (No. 2571.)

Fig. 96. Tubular rhizoid (?) with short branch bearing in relation to a septum a large globular cell (bulbil?) with a shallow nodal disc at its base.  $\times 100$ . (No. 2572.)

Fig. 97. Globular cell (bulbil?) with a nodal disc of small cells, some of which have filamentous growths attached.  $\times 100$ . (No. 2573.)

#### PLATE IX.

#### *Algites (Palæontitella) Cranii.*

Fig. 98. Portion of peaty matrix giving a general view of the appearance of the algal remains. (*a*) filament showing tip; (*b*, *c*) filaments with nodal discs; (*d*) vesicle-like structure.  $\times 50$ . (No. 2546.)

Fig. 99. Portion of same showing septate filaments with contracted dark contents.  $\times 100$ . (No. 2546.)

Fig. 100. Apex of a filament with small terminal cell; this is also seen to the left in fig. 99.  $\times 100$ . (No. 2546.)

Fig. 101. The node with short branch-like protrusions shown at (*b*) in fig. 98. The pointer indicates the node.  $\times 150$ . (No. 2546.)

Fig. 102. The node with rhizoid-like branches shown at (*c*) in fig. 98. The pointer indicates the node.  $\times 150$ . (No. 2546.)

Fig. 103. Rhizoid showing junction of two of the elongated cells.  $\times 150$ . (No. 2388.)

Fig. 104. Another rhizoid showing irregular node of small cells at the junction of two elongated cells.  $\times 150$ . (No. 2388.)

#### *Remains placed with Algites (Palæontitella) Cranii.*

Fig. 105. Portion of peaty matrix showing numerous large thin-walled vesicles (? bulbils) associated with tubular elements with contracted contents.  $\times 12$ . (No. 2475.)

Fig. 106. Two of these vesicles connected together by a nodal cell.  $\times 65$ . (No. 2476.)

Fig. 107. Immature vesicle (bulbil?), beside another only partially shown, with short protrusions from a possible basal node.  $\times 100$ . (No. 2475.)

Fig. 108. Specimen associated with vesicles like those in the preceding figures; it shows an internodal cell and two whorls of branches at the lower and upper nodes.  $\times 100$ . (No. 2476.)

PLATE X.

*Nematophyton Taiti.*

Fig. 109. Portion of a fragment of *Nematophyton Taiti* showing the wide tubular elements and two of the "medullary spots" (*m.s.*).  $\times 50$ . (No. 2523.)

Fig. 110. View of a portion of the preceding specimen.  $\times 100$ . (No. 2523.)

Fig. 111. A portion showing cross sections of the large tubes.  $\times 250$ . (No. 2523.)

Fig. 112. Large tubes bounding a "medullary spot" (*m.s.*) packed with the narrow tubes.  $\times 250$ . (No. 2523.)

Fig. 113. View of one of the sections of the second fragment which shows the peripheral tissues.  $\times 30$ . (No. 2525.)

Fig. 114. Portion of the other section of this specimen.  $\times 50$ . (No. 2526.)

Fig. 115. Portion of fig. 113 showing the inner tubes and the base of the peripheral zone.  $\times 50$ . (No. 2525.)

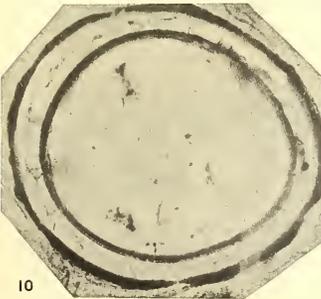
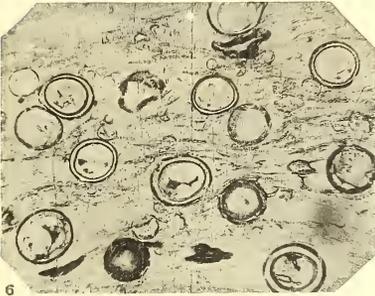
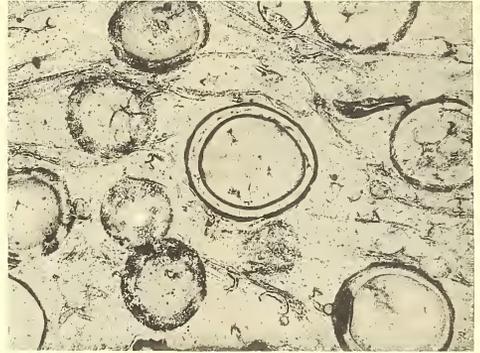
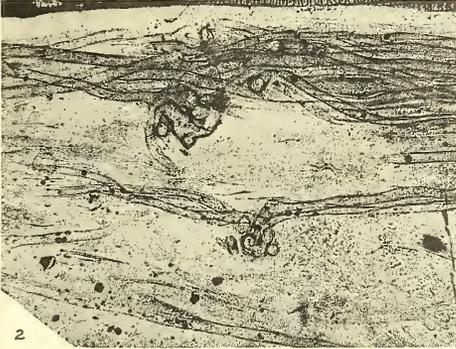
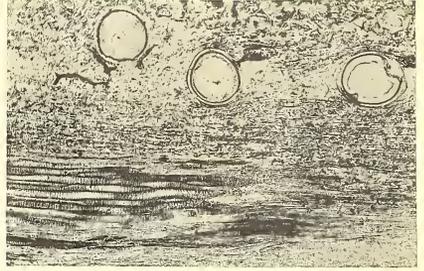
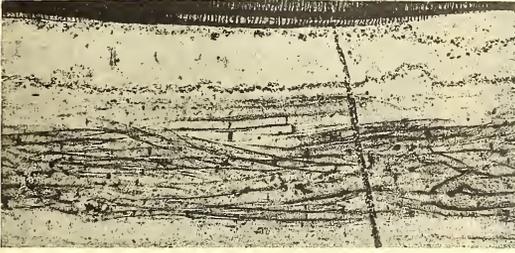
Fig. 116. Portion of the preceding section showing the inner tubes and their relation to medullary spots.  $\times 100$ . (No. 2525.)

Fig. 117. Some of the fine vertical tubes showing the spiral marking of the inner layer of the wall.  $\times 250$ . (No. 2523.)

Fig. 118. One of the inner tubes showing the spiral marking clearly and at places its relation to the outer thick portion of the wall of the tube that has not wholly disappeared.  $\times 250$ . (No. 2525.)

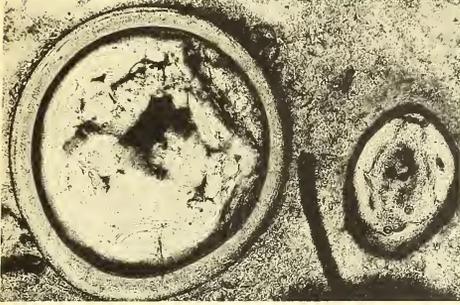
We again gratefully acknowledge our indebtedness to the Executive Committee of the Carnegie Trust for a grant to defray the cost of the plates illustrating this Memoir.

(All the figured specimens in this series of Memoirs are in the collection of Dr R. KIDSTON.)





KIDSTON AND LANG-PLATE II



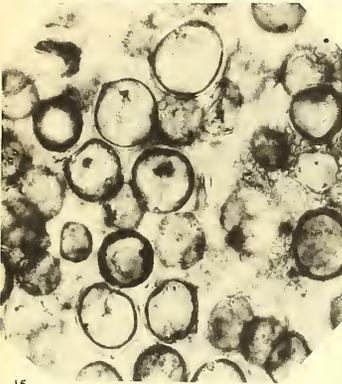
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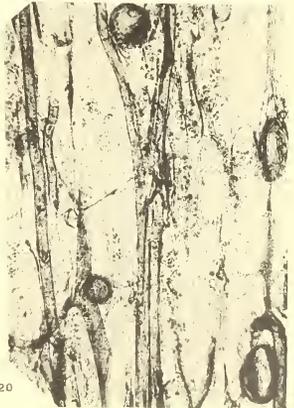
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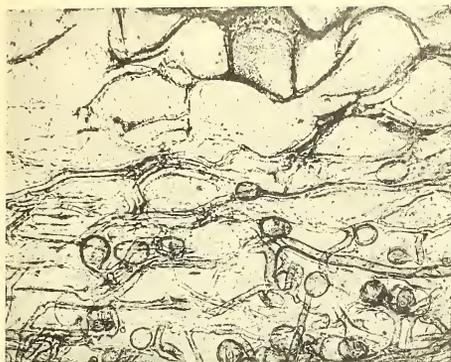


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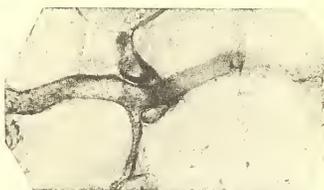
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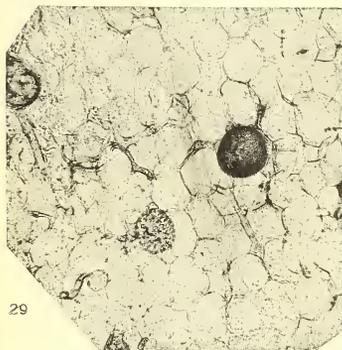
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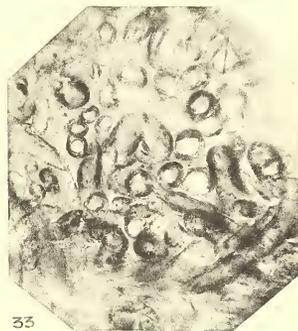
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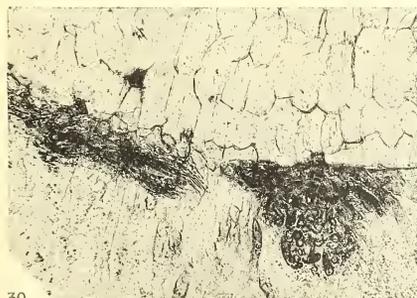
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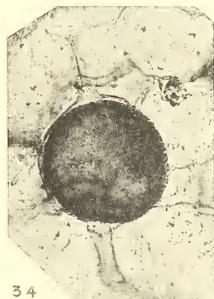
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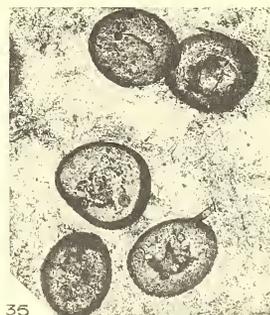
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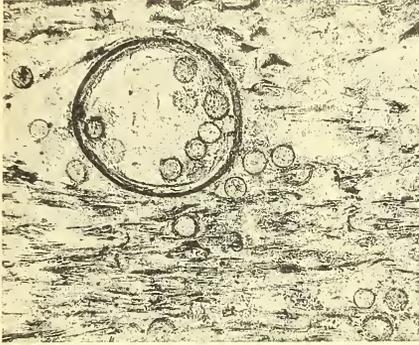
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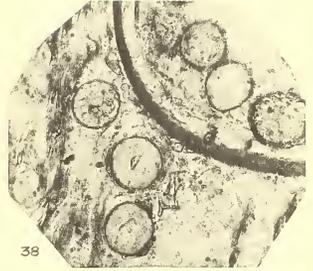
KIDSTON AND LANG - PLATE IV



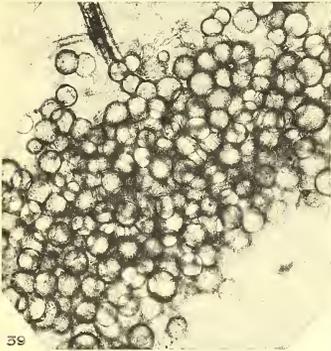
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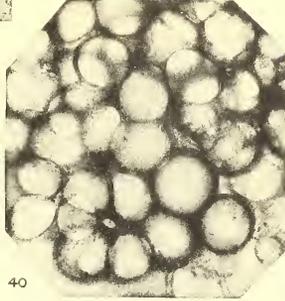
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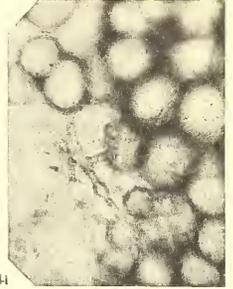
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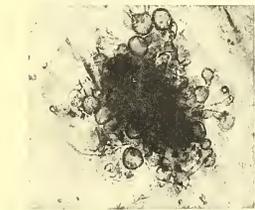
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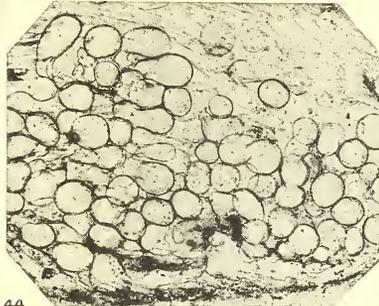
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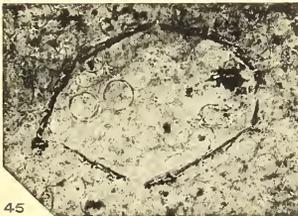
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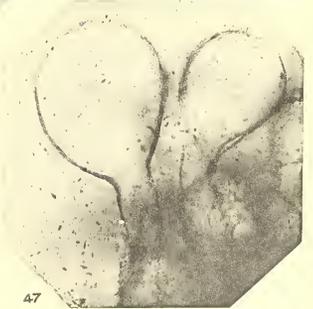
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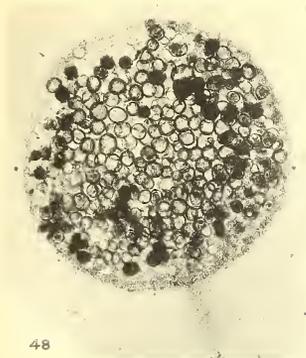


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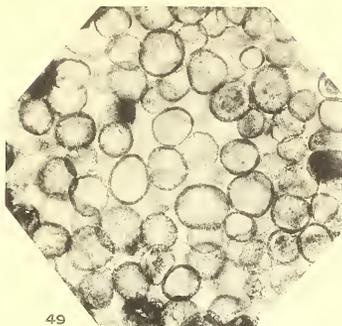


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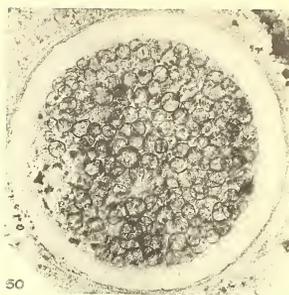




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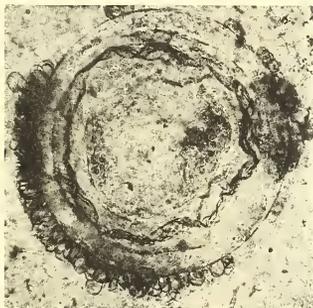
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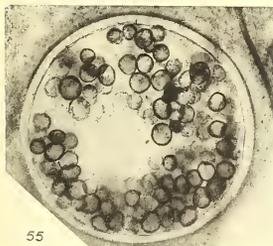
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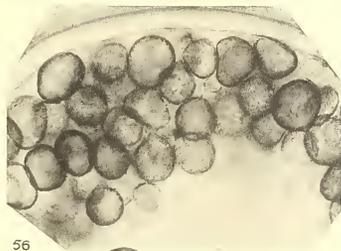
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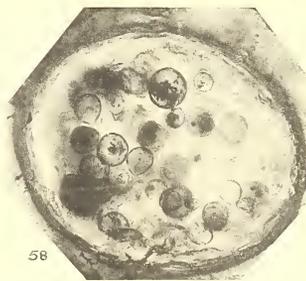
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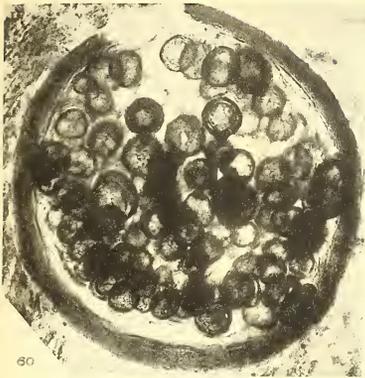
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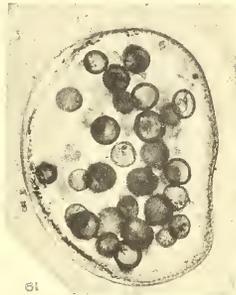
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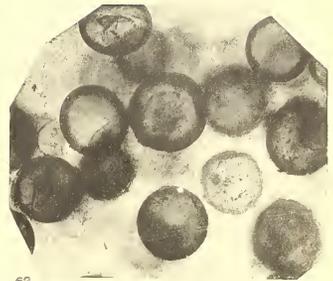
KIDSTON AND LANG—PLATE VI



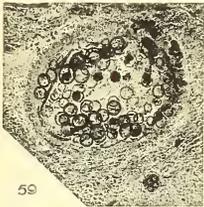
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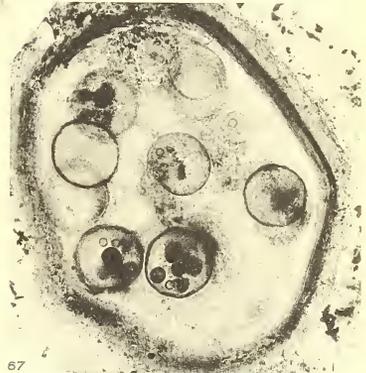
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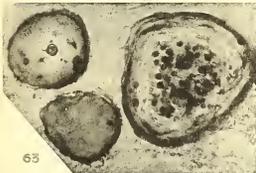
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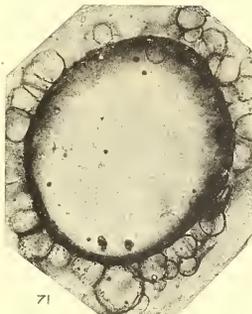
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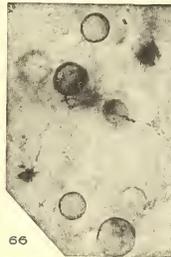
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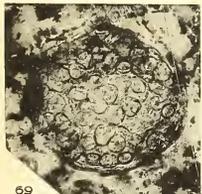
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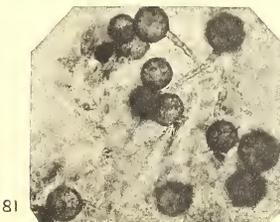
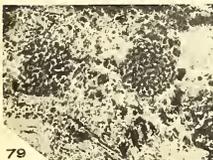
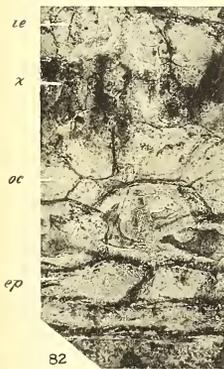
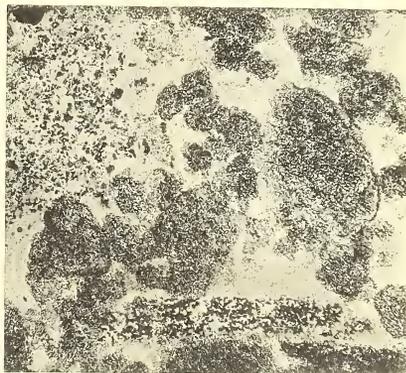
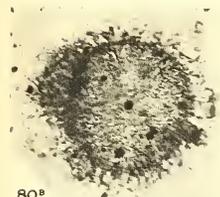
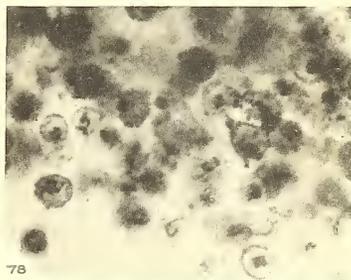
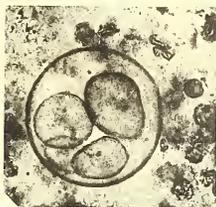
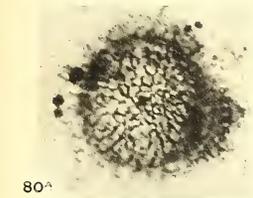
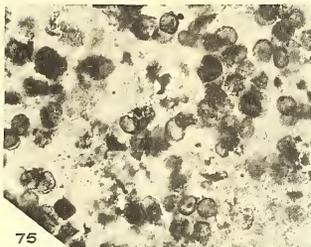
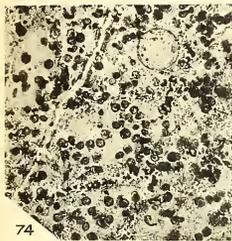
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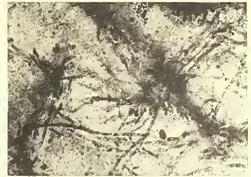
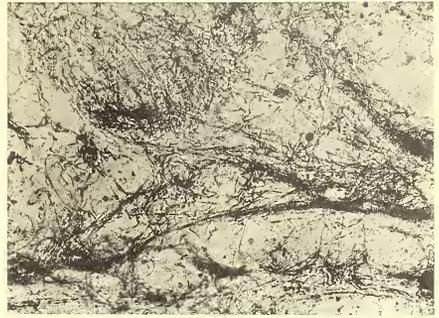
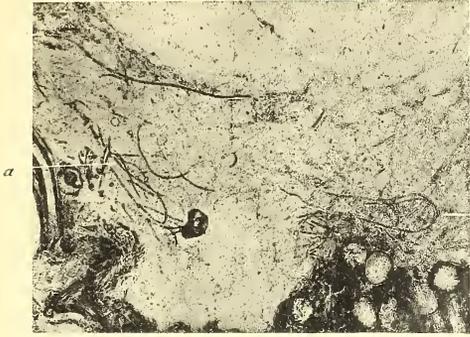


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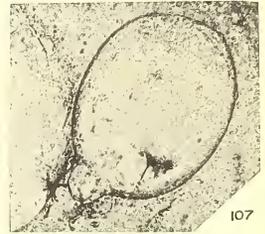
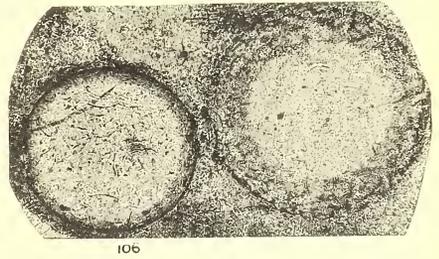
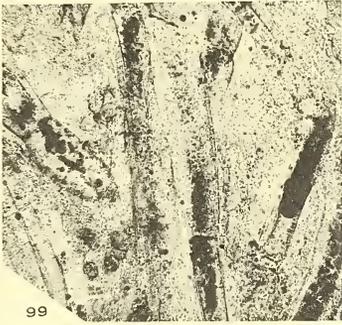
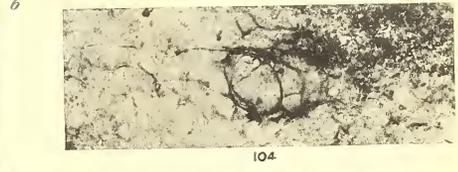
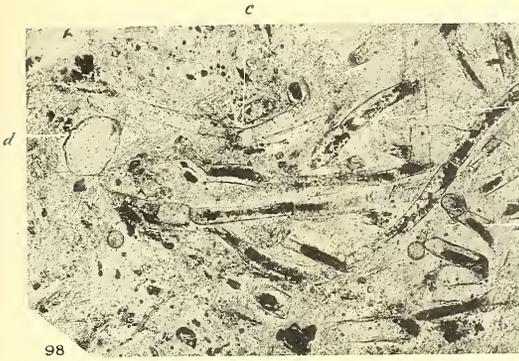


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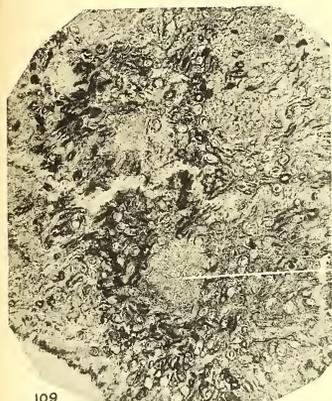


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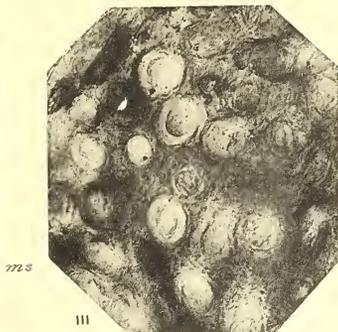




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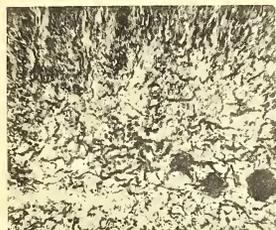
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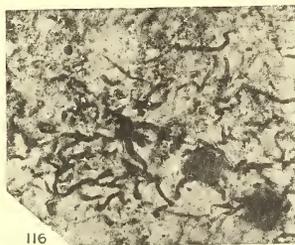
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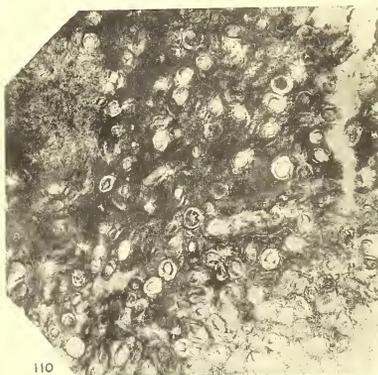
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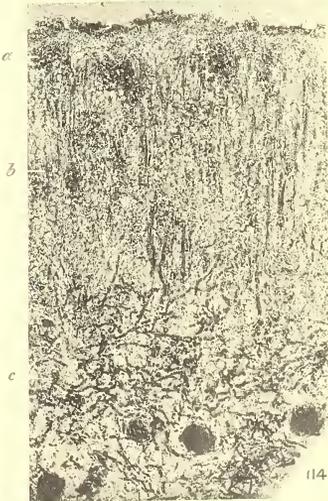
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XIV.	1 5 0	1 1 0	" Pt. 2	1 1 0	0 16 0	" Pt. 2	1 9 6	1 2 5
XV.	1 11 0	1 6 0	" Pt. 3	0 16 0	0 12 0	" Pt. 3	1 11 0	1 3 3
XX. Pt. 1	0 18 0	0 14 0	" Pt. 4	0 7 6	0 5 8	" Pt. 4	0 16 8	0 12 4
XXII. Pt. 2	0 10 0	0 7 6	XXXVIII. Pt. 1	2 0 0	1 10 0	XLIX. Pt. 1	0 7 6	0 7 6
" Pt. 3	1 5 0	1 1 0	" Pt. 2	1 5 0	0 19 0	" Pt. 2	1 12 6	1 4 6
XXVII. Pt. 1	0 16 0	0 12 0	" Pt. 3	1 10 0	1 3 0	" Pt. 3	1 10 0	1 2 5
" Pt. 2	0 6 0	0 4 6	" Pt. 4	0 7 6	0 5 8	" Pt. 4	1 1 9	0 16 0
" Pt. 4	1 0 0	0 16 0	XXXIX. Pt. 1	1 10 0	1 3 0	L. Pt. 1	1 5 9	0 18 9
XXVIII. Pt. 1	1 5 0	1 1 0	" Pt. 2	0 19 0	0 14 6	" Pt. 2	1 7 0	1 0 0
" Pt. 2	1 5 0	1 1 0	" Pt. 3	2 3 0	1 11 0	" Pt. 3	1 7 0	1 0 0
" Pt. 3	0 18 0	0 13 6	" Pt. 4	0 9 0	0 7 0	" Pt. 4	1 2 0	0 17 0
XXIX. Pt. 1	1 12 0	1 6 0	XL. Pt. 1	1 5 0	0 19 0	LI. Pt. 1	1 5 0	0 19 0
" Pt. 2	0 16 0	0 12 0	" Pt. 2	1 12 6	1 5 6	" Pt. 2	1 13 0	1 5 0
XXX. Pt. 1	1 12 0	1 6 0	" Pt. 3	1 6 0	0 19 6	" Pt. 3	1 15 0	1 6 0
" Pt. 2	0 16 0	0 12 0	" Pt. 4	1 0 0	0 16 0	" Pt. 4	1 11 6	1 3 6
" Pt. 3	0 5 0	0 4 0	XLI. Pt. 1	1 1 0	0 15 9	LII. Pt. 1	1 7 0	1 0 6
" Pt. 4	0 7 6	0 5 8	" Pt. 2	1 9 6	1 2 0	" Pt. 2	1 10 0	1 2 0
XXXI.	4 4 0	3 3 0	" Pt. 3	2 5 0	1 13 6	" Pt. 3	2 3 0	1 11 6
XXXII. Pt. 1	1 0 0	0 16 0	XLII.	2 2 0	1 11 0	" Pt. 4	2 13 0	2 0 0
" Pt. 2	0 18 0	0 13 6	XLIII.	2 2 0	1 11 0			
" Pt. 3	2 10 0	1 17 6	XLIV. Pt. 1	1 18 6	1 9 0			
" Pt. 4	0 5 0	0 4 0	" Pt. 2	1 1 0	0 15 9			
XXXIII. Pt. 1	1 1 0	0 16 0	XLV. Pt. 1	1 9 0	1 2 0			
" Pt. 2	2 2 0	1 11 0	" Pt. 2	1 7 0	1 0 0			
" Pt. 3	0 12 0	0 9 6	" Pt. 3	1 13 9	1 5 3			
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