XI. *On* Asterochlænopsis, *a New Genus of Zygopterid Tree-Ferns from Western Siberia.*

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(*Communicated by* Prof. A. C. Seward, *F.R.S.*)

(Plates 49–51.)

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Contents.

Introduction.

About fifty years ago a Swedish engineer picked up a silicified stem* near Semipalatinsk, in the Kirgis Steppes in Western Siberia. The fossil was cut transversely into several slabs, at least five of which ultimately found their way to Germany. One of the pieces reached the hands of K. G. Stenzel of Breslau and he described it in 1889 under the name *Asterochlæna* (*Clepsydropsis*) *kirgisica*†. Another fragment came into the hands of A. Schenk, then professor of botany at Leipzig, and apparently in ignorance of Stenzel's fossil, he described it in the same year under a distinct name, *Rachiopteris*

* Along with this fossil, the stem of another plant, now known as *Steloxylon ludwigii*, was also found, but with this specimen we are not here concerned, although it also has an interesting history of its own.

† Stenzel (1889). The original is in the Mineralogical Museum at Dresden.

ludwigii LEUCKART and SCHENK*. The ultimate sources of the two specimens are so nearly identical that the present writer, in a paper published in 1919,† suggested that they were probably pieces of one and the same stem. This suspicion was recently confirmed in an indirect way by Prof. KARL WANDERER of Dresden (see below), and since then all doubt on the matter has been removed by a direct comparison of the two type-specimens, which have been found to fit against each other.

Besides these two fragments it has been possible, during a recent tour in Europe, to relate to the same original stem three other pieces, one of which was preserved in Dresden, one in Chemnitz and the third in Breslau. The Breslau fragment, originally in the possession of GOEPPERT, was mentioned by STENZEL in his memoir, already cited above ; the other two specimens do not appear to have been noticed in the literature (see text-fig. 1).

Thanks to the generosity of Prof. WANDERER,Director of the Mineralogical Museum in Dresden, and of Dr. ERICH STRAUSS, of the Städtisches Museum in Chemnitz, three of the specimens have now been examined for the first time in thin sections, with the result that some unexpected features have come to light. They lead to the conclusion that this Siberian zygopterid originally referred to *Asterochlæna*, but latterly regarded, on account of its petiolar strand, as a species of *Clepsydropsis*, is in reality a plant allied to *Asterochlæna* but distinct from any of the known genera of Zygopterideæ. The final shape of the foliar strand was already known to be of the *Clepsydropsis* type, but the leaf-trace in some of its earlier phases recalls that of *Asterochlæna* more than any other zygopterid. The stele of the leaf-bearing axis, hitherto practically unknown, has been found preserved, although only partially, in the Chemnitz specimen. It is of a new type, intermediate between *Ankyropteris* and *Asterochlæna :* there is a stellate " mixed pith " with numerous rays, but there is no indication of the spidery arms so characteristic of the latter genus.

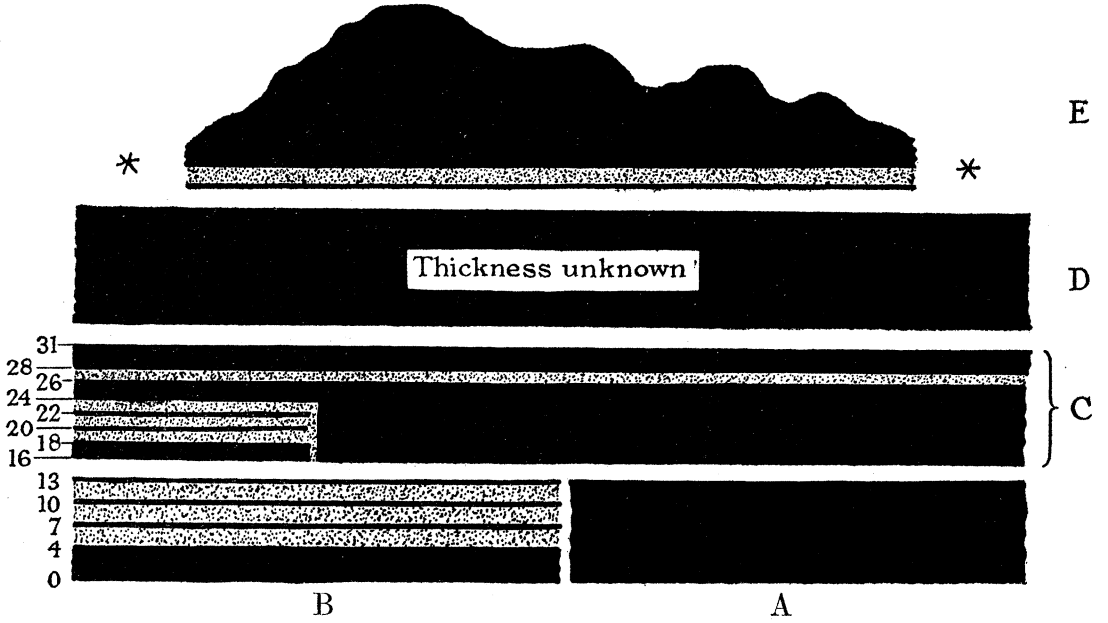
This combination of characters seems to leave no doubt that the plant can no longer be retained as a species of *Clepsydropsis* and that it should be placed in a new genus. For this the name *Asterochlænopsis* is proposed. Incidentally, the present case will be a useful warning that the final form of the petiolar bundle in the Zygopterideæ, if considered by itself, may be very misleading ; the more so as our present classification of the family is necessarily based chiefly upon this character.

It may be of some interest to state briefly the circumstances in which the scattered fragments of ÅBERG'S original were brought together for the present re-investigation.

* SCHENK (1889), Plate 3, fig. 50. The species was named after LUDWIG of Darmstadt, who had received the fossil from the original discoverer during a journey in Siberia, and had later brought it to Germany. After LUDWIG'S death in 1880 the fossil passed into the hands of LEUCKART, a druggist and factory owner of Chemnitz, in whose private collection it remained till it was transferred to the Botanical Institute at Leipzig, and became the type-specimen of SCHENK'S species. See GOEPPERT u. STENZEL (1881), p. 126. SCHENK'S type-specimen is at present in Leipzig.

† SAHNI (1919), p. 83, footnote.

The starting point was a desire to compare the northern forms referred to *Clepsydropsis* with the Australian Zygopterid, in which a *Tempskya*-like false stem was recently described.* In their petiolar anatomy *C. antiqua*† and the Siberian form are so similar to the Australian that the question naturally arose whether they also showed a Tempskyoid condition, or whether this was a peculiarity of the southern species. So far as *C. antiqua* is concerned the question must for the present remain unanswered, because nothing is yet known of the leaf-bearing axis. But knowing from STENZEL's‡ work that



TEXT-FIG. 1.—Diagrammatic vertical section to show the relations of the different fragments of the Kirgis Zygopterid. The figures on the left indicate in millimetres the levels of the thin sections and polished faces. A is SCHENK's type-specimen of "*Rachiopteris ludwigii*" (Bot. Inst. Leipzig); B is LANGE's fragment (Min. Mus. Dresden); C is STENZEL's type-specimen of "*Asterochlæna* (*Clepsydropsis*) *kirgisica*" (Min. Mus. Dresden); D is GOEPPERT's fragment (Geol. Mus. Breslau); E is No. 96 of the LEUCKART Collection (now in the Städt. Mus. Chemnitz). This last piece is incomplete at * *. The portions of the stem below A and B are unknown. The top end as well as the sides show unmistakable signs of wind-erosion, the surface being very uneven but polished. Nat. size.

the type-specimen of *Asterochlæna* (*Clepsydropsis*) *kirgisica* includes at least a fraction of the stem, I was prompted to apply for a loan of the fossil, preserved at Dresden. As the specimen was then thought to be unique, the whole of it could not be sent abroad, but Prof. WANDERER kindly sent me (in 1926) a slice, about 7 mm. thick, cut from one corner of it. This was very useful for a comparison of the root and petiolar anatomy

* SAHNI (1928).

† UNGER (1856), Plate 7, figs. 1–9; BERTRAND (1909); BERTRAND (1911 *a*).

‡ STENZEL (1889), Plate 4, fig. 38.

(Plate 50, figs. 4–7), but as it did not include the stem, my chief object still remained unfulfilled. However, in May, 1928, I received from Prof. WANDERER a very interesting letter, in which he informed me that in an old private collection (Sammlung Lange) purchased by the Museum, he had just chanced upon a specimen labelled "*Rachiopteris ludwigii* LEUCKART u. SCHENK. Fundort: Semipalatinsk (Sibirien)." He added that according to the catalogue the previous owner had obtained the fossil from a certain Mr. SCHENK; and that a comparison of this fragment with STENZEL'S type-specimen showed beyond doubt that the two were not only specifically identical, but fragments of one and the same stem. On placing the two fragments together Prof. WANDERER had found that LANGE'S specimen exactly coincided with one half of the lower surface of STENZEL'S original.

Now that two pieces of the Kirgis species were available Prof. WANDERER willingly sent me the smaller one for investigation. From this piece (Plate 1, fig. 1) three serial cross-sections were prepared by hand at Lucknow, and the following description and figures are chiefly based upon these.

LANGE'S fragment was at first thought to be the original of SCHENK'S figure, but a comparison with the latter at once showed that this was not the case. It was, in reality, a hitherto unknown piece, broken off from an originally complete slab of which only one half had been figured by SCHENK. In response to my request, Dr. R. GIESSLER, Curator of the Botanical Institute at Leipzig, very kindly sent to me on loan (November, 1929) the figured specimen,* and as expected the two fragments were found to fit into each other along their broken edges (see text-fig. 2). The two quadrants together made up a semi-circular slab coinciding exactly with the *whole* lower face of STENZEL'S original.

An examination of LANGE'S specimen (Plate 1, fig. 1) not only made it probable that the plant had a simple axis like that of an ordinary tree-fern, but showed it to be anatomically more of an *Asterochlæna* than a *Clepsydropsis*. Subsequently, while I was on a visit to Germany, Prof. WANDERER very generously also placed STENZEL'S original at my disposal (August, 1929); and a glance at this specimen was enough to confirm the conclusion just expressed: there was neither any indication of a *Tempskya*-like stem organisation, nor any other particularly close resemblance with the Australian Zygopterid, except in the form of the petiolar trace.

With STENZEL'S original and LANGE'S fragment in my possession I passed on from Dresden to Chemnitz (September, 1929) and was surprised to find, in the Städtisches Museum,† a third specimen, hitherto undescribed, which by its form, colour and mode of preservation at once struck me as being another fragment of the same Kirgis stem.

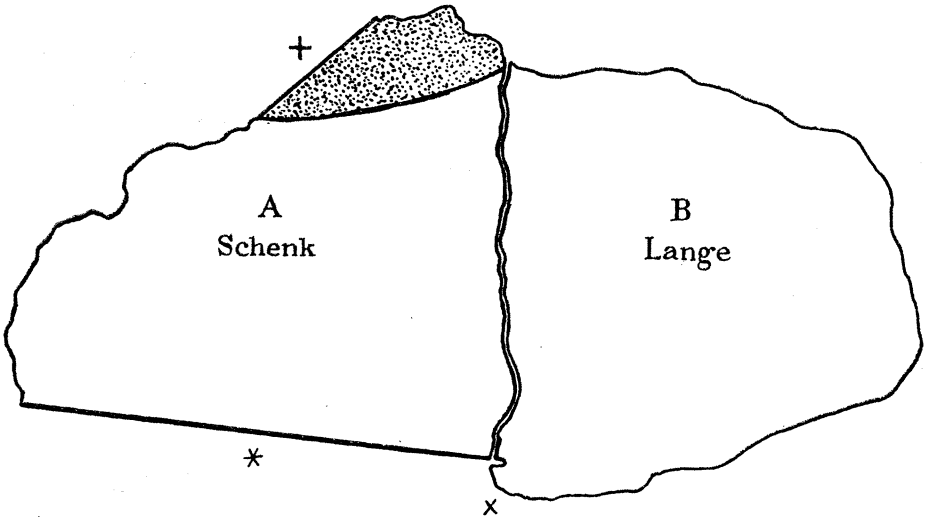
* SCHENK (1889), Plate 3, fig. 50. The labels accompanying this specimen read as follow: "*Tubicaulis* (?) *ludwigii*. Farnstamm, zwischen Akmolinsk und Semipalatinsk in der Steppe der Kirgisen auf Felsitporphyr, unter welchem Steinkohlen liegen, gefunden. R. LUDWIG"; and "*Zygopteris* = *Rachiopteris ludwigii* LEUCKART et SCHENK (*Tubicaulis*, Cotta), Siberien. Semipalatinsk. LEUCKART."

† Previously known as the König Albert Museum.

Of special interest was J. T. STERZEL'S label accompanying the fossil, which read as follows :—

" *Rachiopteris ludwigii* LEUCKART et SCHENK. Aus Rotliegendem (?). Bei Semipalatinsk, Kirgisensteppe (Asien). Leuckart'sche Sammlung Nr. 96. Ueber Medullosa etc. 1889, Taf. III, fig. 50. *Asterochlæna* (*Clepsydropsis*) *kirgisica* STENZEL,' Tubicaulis ' 1889, S. 20, Taf. IV, fig. 38-44."

Evidently, the identity of the two species was already known to STERZEL, who was for many years Director of the Museum, till his death in 1914. I am not aware that either STERZEL or anyone else has ever published the fact of this identity. One face of this specimen showed the weathered upper end of the stem as originally found in Siberia, the other had been cut and polished. On placing this slab on top of STENZEL'S, I found that, while there seemed no doubt of their being parts of one and the same stem, the two faces did not quite coincide as contiguous sections should do : apparently an



TEXT-FIG. 2.—Outline sketches of fragments A and B as seen from above to show how they fit together along a median crack. The longitudinal section at * must have been removed before the slab broke into two, for the cut extends into the fragment B. Another longitudinal section was removed at +, and a transverse one from the shaded area. The stem stele is confined to the corner × of B. Nat. size.

intermediate slice was missing. This missing slice is no doubt the one originally in the possession of GOEPPERT at Breslau, which STENZEL mentioned in his memoir* and which was examined more recently by Prof. PAUL BERTRAND.† As I was unable to visit Breslau, Prof. GOTHAN very kindly requested, on my behalf, a loan of this specimen from the Geological Museum. Unfortunately, the fossil has not been found, but I owe to the kindness of Prof. BERTRAND, to whom I next applied for information, two old photographs prepared by him in 1907. These photographs show the upper and lower polished faces of GOEPPERT'S fragment, and a comparison of these with the upper

* STENZEL (1889), p. 1.

† BERTRAND (1909), p. 203.

face of STENZEL's original and with the lower face of the Chemnitz specimen proves conclusively that this is, indeed, the missing middle piece.*

Of the original fossil, as discovered by ÅBERG, at least five pieces are thus known to have existed : two at Dresden and one each at Chemnitz, Leipzig and Breslau. The relations of the five pieces with each other, and the positions of the thin sections cut from some of them, are shown diagrammatically in text-fig. 1 (see also text-fig. 2). It will be seen that while the upper part of the original stem has been accounted for by the five fragments, portions at the base are still missing. They may turn up later in some museum or private collection, but the most important pieces, because of the stem stele included in them, are those at Chemnitz and Breslau.

As a considerable part of this work was done during a tour on the Continent, the number of those to whom I am indebted in various ways is large. My best thanks are due to Prof. WANDERER of Dresden, Dr. STRAUSS of Chemnitz, and Dr. GIESSLER of Leipzig, for the loan of the different specimens for investigation ; to Prof. PAUL BERTRAND of Lille for the useful photographs of GOEPPERT'S specimen, and to Prof. GOTHAN of Berlin and Dr. K. RODE of Breslau, for their efforts in connexion with this missing Breslau fragment. I wish to thank Fräulein L. ADAMETZ, Secretary to the Natural History Museum in Vienna, for facilities in preparing photomicrographs and for much other assistance, and Geheimrat Prof. GOEBEL and Prof. MAX HIRMER for facilities of work at the Nymphenburg Laboratory at Munich.

For permission to examine various specimens and sections of Zygopterideæ (including many originals) during the tour I am indebted to the authorities of the Geolog. Bundesanstalt (formerly Reichsanstalt) at Vienna ; to Dr. Fr. NĚMEJC, Keeper of the palæobotanical collections at the National Museum in Prag ; to Prof. WANDERER of the Mineralogical Museum (Zwinger) in Dresden ; to Dr. STRAUSS of the Städtisches Museum in Chemnitz ; to the authorities of the Geological Institute of the Bergakademie at Freiberg i. S. ; to President P. KRUSCH and Prof. GOTHAN of the Prussian Geological Survey in Berlin, and to Dr. JULIUS SCHUSTER of the Museum für Naturkunde at the University of Berlin. I am grateful to Dr. D. H. SCOTT for opportunities of discussing several points arising out of my work on " *Clepsydropsis* " *australis*, as well as during the present investigation. Lastly, it is a pleasure to express my gratitude to Prof. A. C. SEWARD, in whose laboratory the work has been completed, and with whom I have had the privilege of discussing some of the theoretical results.

Previous Work.

The published work on the plant is confined, so far as I know, to the two papers by STENZEL and SCHENK, already cited. As the two specific names appeared in the

* Since the above was printed I have been able to visit Breslau, where I found the missing fragment. The slab is 13 to 14 mm. thick (text-fig. 1, D), and on the upper face a portion of the stele is preserved, as in the Chemnitz specimen. I wish to express my sincere thanks to Prof. Dr. Soergel for permission to examine this as well as other specimens in the Goeppert Collection.

same year (1889) the question of priority is not easy to settle, for the exact date of publication is known only for SCHENK's paper.* The fact that J. T. STERZEL's label accompanying the Chemnitz specimen gave *kirgisica* as a synonym, seems to indicate that the specific name *ludwigii* has priority, but for this there is no conclusive evidence ; and I have not been able to ascertain any further facts bearing upon the point at issue. However, the question is of no great importance, and need not detain us here.

STENZEL's description is fuller, and his figures are much more accurate than SCHENK's. As a part of the leaf-bearing stem was included in STENZEL's specimen, he was able to indicate the affinity with *Asterochlæna laxa*, which he was describing at the same time. SCHENK, on the other hand, having only the petioles at his disposal, referred his fossil to the artificial genus *Rachiopteris*, although he recognised the resemblance with *Clepsydropsis*. His figure of the specimen is inaccurate. Not only is the orientation of the petiolar strands quite different from that shown in the figure, but even the contour of the specimen is incorrectly drawn. It does seem strange that, having originally had in his possession a complete slab like that of STENZEL, SCHENK should have given away to LANGE the more important half, which included the stem. Had SCHENK figured the entire slab, his sketch would have been so similar to STENZEL's figure at the adjoining fragment, that the relation of the two specimens with each other would not so long have remained obscure.

We need not go into details over the structural facts described by SCHENK and STENZEL. STENZEL's fig. 38, Plate IV, is a remarkably good sketch of the upper face of the slab (level 31 mm. in text-fig. 1) ; he correctly draws the outline of the leaf-bearing stem with the decurrent leaf-bases, including the fragments of the stele marked *sg*, *sg'* in his figure. The leaf-traces in the cortex are merely shown as dots.† In one of the free petioles‡ he shows a strand with a slight adaxial curvature ; this is an error, for none of the leaf-strands ever show any curvature. The petiole marked *b* in his figure has only a single strand in the appendage on the left, not a pair, as indicated in the sketch.§ For the rest, the figure is remarkably faithful to the original.

From SCHENK's type-specimen three thin sections (two longitudinal sections and a partial transverse section) appear to have been made, and SCHENK probably examined these, for he refers to such microscopic details as root-hairs and scalariform thickenings on the tracheides. These sections have not been seen by me, and I do not know if they exist any longer.

* SCHENK submitted his manuscript on March 4, 1889 ; the paper was printed on May 20, and published in June of the same year. STENZEL, in one of his later papers (1896, p. 30), states, in another connexion, that his manuscript was sent in as early as June 4 of the previous year, but he does not mention the date of publication, which alone is to be considered.

† A few of the leaf-traces on the lower face (level 16 mm.) clearly show the *Dineuron*-like stage (*cf.* Plate 51, figs. 17–23), and there is also a trace about to come off from the stele. This face was not figured by STENZEL.

‡ The petiole situated about 2 cm. above the letter *w'* in his fig. 38.

§ A point on which Prof. P. BERTRAND (1909, p. 203, footnote) also had just doubts.

Description.—Gross Features.

A naked-eye inspection of the polished faces and thin sections, helped with a pocket-lens, shows most of the important features of the fossil. The external surface, best seen in the Chemnitz specimen, is very uneven, but smooth and polished in such a way as to suggest wind- rather than water-erosion* ; it is quite unlike the surface of a rolled pebble.

One sees at a glance that the fossil must have been a tree-fern of considerable size. Assuming that the trunk was cylindrical, the fragment figured by STENZEL represents a sector including a little more than a third of the entire cross-section, which must have been at least 15 cm. in diameter. This does not take into account an unknown thickness removed by decortication, which may have included a felt of adventitious roots.

The best preserved petioles are in a thick peripheral zone of dark brown colour ; the stands are mostly preserved in their natural positions and show the typical *Clepsydropsis*-life form. The spaces between the petioles are packed with adventitious roots and aphlebiæ ; here, the roots are mostly seen in transverse section, and must have grown vertically downwards. The larger roots may attain a diameter of 5 or 6 mm., but as a rule they are only about 2—3 mm. thick. The finer branches may easily be confused with aphlebiæ.

The lighter-coloured central region of the trunk, which must have been comparatively soft, is on the whole badly preserved, except (luckily) for the vascular tissues. The decurrent parts of the petioles are only 5 to 7 mm. thick ; where they become free from the stem they have increased to about 8 mm. ; above this point they increase more gradually in size, till in the most distal parts preserved they reach a diameter of 11·5 mm. Fragments of the stem-stele are to be seen in all three specimens, but there is more of it in the Chemnitz piece than in the others,† and with a hand-lens one sees at once that the structure is distinct, although not radically different, from that of all other zygopterids.

The stele may be described as representing a type intermediate between *Asterochlæna* and *Ankyropteris*. It is differentiated into an outer zone, consisting entirely of tracheids, and a stellate core which corresponds to the " mixed pith " of *Ankyropteris* or " *Clepsydropsis* " *australis*. But the " pith," to judge by the small fragment available, is produced into many more rays than five, which is the number characteristic of the Australian plant and of several species of *Ankyropteris*. From *Asterochlæna*, the stele

* Both Prof. WANDERER and Prof. SEWARD, who have examined the fossil, agree that such a surface cannot have been due to water action. STENZEL'S view (1889, p. 21) repeated by SOLMS (1910, p. 542), that the fossil is a rolled pebble does not seem to be tenable. GOEPPERT, it is true, states that the fossil was found in an alluvium (see GOEPPERT u. STENZEL, 1881, p. 126), but this does not seem to follow from LUDWIG'S letter, which he quotes.

† The photograph of the upper face of the Breslau specimen shows that this fragment also contains as much as the stele as the Chemnitz fragment, which is contiguous to it.

differs in the absence of the long spidery arms so characteristic of that genus, and in the much greater development of the " mixed pith."

As stated, the final form of the petiolar trace is decidedly like that of *Clepsydropsis*. There is not the least sign of a curvature, and the peripheral loops are so placed that the strand has two planes of symmetry, one radial (anteroposterior), the other tangential. In view of these facts, it is surprising that the leaf-trace at its origin is a solid or nearly solid strand, and the peripheral loops usually do not make their appearance till after the protoxylem has bifurcated. There is thus no stage quite corresponding to the flattened ring of " *C.*" *australis*, nor is there at any time the remotest sign of a curvature in the leaf-trace. The different stages in the formation of the leaf-trace can be followed in a single cross-section of the trunk by comparing strands more or less removed from the stele. As we have seen, some of these stages recall the condition in *Asterochlæna*,* but the details will be described later. The supply to the appendages of the primary rachis arises in very much the same manner as that described for " *C.*" *australis* ; the structure and mode of branching of the aphlebiæ is also very similar.

The roots in the central region of the trunk are mostly seen in more or less oblique longitudinal section, only a few being cut transversely. They take their origin in the leaf-bearing axis between the leaf-bases, and at first run almost horizontally, but later turn obliquely downwards and outwards. On reaching the peripheral zone, they appear to bend directly downwards. The conditions are thus closely similar to those described in " *C.*" *australis*, and the existence of an external felt of roots seems very likely. As in the Australian plant, moreover, the older petioles frequently show intrusive roots, although they are never seen in such large numbers. There is no reason to doubt that here, too, the intrusive roots belong to the plant in whose petioles they are found, and we may take it that they effect their entry through the upper ends of old rachis-sheaths, as in " *C.*" *australis*. The structure of the roots is very similar to that in the latter species, but they seem to attain to a much larger size.

We thus see that in the anatomy of the root, petiole and aphlebiæ, the Siberian plant closely resembles the Australian. The two tree-ferns may also have been rather similar in external appearance, although no doubt the northern form was built on a smaller scale. But the stele, as we have seen, is different, and in the crowded phyllotaxis, as well as in the slightly abaxial origin of the pinna- or aphlebia-traces, the Siberian plant approaches *Asterochlæna*.

Detailed Description.

(i) *The Stem.*—Figs. 1, 2, Plate 49, show all that is preserved of the leaf-bearing axis in LANGE'S specimen. The cortex, consisting of small rather thick-walled cells, shows several leaf-traces more or less removed from the stele. Some of these have cortical sheaths of their own already differentiated round them, others lie in decurrent leaf-bases in various stages of separation from the stem. A fragment of the stele is preserved at

* The earlier stages show interesting points of resemblance with the corresponding stages in *Zalesskya* and *Thamnopteris*. See text-fig. 4 B.

the edge of the specimen; at *i.l.t.* in Plate 49, fig. 2, is an incipient leaf-trace with a single central protoxylem.

Figs. 3, 10, 11 on Plates 49, 50, 51 are from a section of the Chemnitz specimen. It is a pity that more of the stele is not preserved, but there is enough to show that, while it was fundamentally similar to that of several other zygopterids (*cf. Ankyropteris scandens*, " *Clepsydropsis* " *australis*, etc.) in having a xylem cylinder enclosing a stellate " mixed pith," it is not quite like any of the known types of stele in this family, and helps to distinguish the genus.

The xylem cylinder is a little over a millimetre in radial thickness, and seems to consist only of tracheides. Although a thin longitudinal section is not available, the inner broken face of STENZEL'S specimen is a fairly good longitudinal fracture of the xylem cylinder. Examined with strong reflected light under a binocular microscope it shows numerous beautifully preserved scalariform tracheides, of exactly the same type as those figured by me in the stem and petiole of " *C.*" *australis*.* They are of various diameters, but even the narrowest are scalariform.

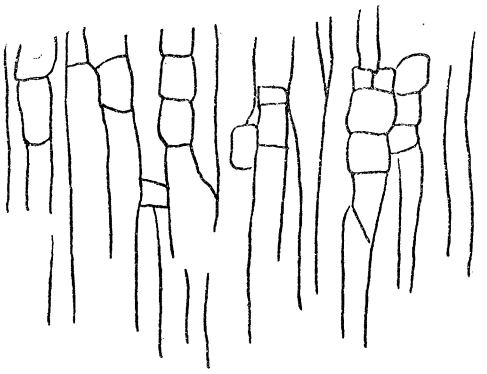
In the fragment of the stele shown in figs. 3, 10, 11 the xylem cylinder is traversed in five places by thin rays from the relatively large " pith." Some of the rays are longer than others, but none of them ever go right through the xylem. Two of them (marked 2 and 5 in fig. 10) are seen to penetrate deeper than the others, and these are related to two leaf-traces in different stages. The trace on the right (No. 5) is nearly ready to come off, and shows a central cavity lined by narrow tracheides, which probably surrounded an island of tissue similar to the " pith."

The well-preserved " pith " consists of a mixture of wide and narrow cells. The wider cells are relatively few and lie scattered in a ground-work formed of the narrower cells. A good longitudinal fracture of the " pith," flanked on either side by two strips of the xylem-cylinder, is seen on the inner surface of the Chemnitz specimen, and yielded the camera-lucida sketch reproduced in text-fig. 3. The large cells are more or less isodiametric, the small ones are much narrower and elongated, with transverse or oblique ends. Expecting the latter to be xylem elements, I searched carefully for any sculpturing, but found none. This may, however, be due to the preservation, for I failed equally to detect any sculpturing in the undoubted xylem elements composing the strips right and left of the " pith." In any case, there seems no doubt that the narrow-celled rays projecting into the xylem cylinder are composed chiefly or entirely of scalariform tracheides. They correspond to the so-called protoxylem bands of *Asterochlæna*, from the ends of which the protoxylems of successive leaf-traces are nipped off.

To judge by the small fragment of the stele which is preserved, the entire stele must have had well over a dozen rays. This multiradiate condition obviously goes hand in hand with the more crowded phyllotaxis, as compared with forms like *Ankyropteris* and " *Clepsydropsis* " *australis*. As we know from Prof. PAUL BERTRAND'S splendid

* SAHNI (1919), Plate 4, figs. 4, 7; (1928), Plate 3, fig. 14.

monograph on *Asterochlæna laxa*,* the same feature is seen in a somewhat different form in that related type. In this case the numerous ultimate rays which give off the leaf-traces are formed by the branching of a few primary rays.



TEXT-FIG. 3.—Part of the central tissue as seen in a longitudinal fracture of the stele in the Chemnitz specimen. Drawn with the help of a camera-lucida under strong reflected light. The squarish cells, tending to be placed in vertical rows, are either parenchymatous tracheides or ordinary parenchyma cells; the elongated cells are no doubt xylem elements, although no sculpturing could be made out. × *ca.* 45.

A certain general resemblance may also be noticed with the steles of the Permian Osmundaceæ *Thamnopteris* and *Zalesskya*, and of a fern from the Permian of Chemnitz, described under the name *Protothamnopteris baldaufi*,† although the structure is not sufficiently known to show how far the comparison holds good.

(ii) *The Leaf.*—The leaves must have been of great length and stood almost erect, for the petiole bases are very nearly parallel to the stem, and the leaf-traces diverge only very gradually from the stem stele. As figs. 3, 5, 6 show, the structure of the petiole and of the fully formed leaf-trace is very similar to that in "*C.*" *australis*. The cortex is in three zones. The inner cortex is usually crushed and appears to have been composed of a delicate tissue. The middle zone of large thin-walled cells grades into the smaller-celled, almost sclerenchymatous tissue forming a sheath to the petiole. There appears to be no well-marked epidermal layer. No emergences have been seen, but this may be due to the preservation; or they may have fallen off from the basal parts of the rachis. Neither stomata nor lenticels have been observed; in fact, the cortex appears to have been devoid of intercellular spaces.

The cross-section of the *fully formed petiolar strand* has roughly the same shape as in *C. antiqua* and "*C.*" *australis*, but the "waist" is more constricted and the ends are rather more swollen, so that the form is more dumb-bell-like, at least in a few of the

* BERTRAND (1911*a*).

† BECK (1920), Plate 2, fig. 5. Prof. HIRMER (1927), p. 538, has transferred the species to the genus *Grammatopteris*, a step which seems to be justified by the structure of the leaf-trace. I am deeply indebted to Prof. Dr. Schumacher, of the Bergakademie in Freiberg i.S., for a loan of the type specimen, which I hope to describe more fully at a later date.

outermost petioles (see Plate 49, fig. 3). The average dimensions of the petiole and strand in the peripheral part of the trunk are given below :—

Cross-section of petiole : 10 mm.

Cross-section of petiolar bundle : length, 3·75 mm. ; thickness at the " waist," 0·65 mm.

The *lateral appendages of the rachis* are very similar in their structure and mode of branching to those figured by Dr. SCOTT* in *Ankyropteris corrugata*, and to those more recently shown in " *Clepsydropsis* " *australis*. It is difficult to say whether these organs should be called pinnæ or aphlebiæ. As Dr. SCOTT† has observed, there is considerable analogy between the two ; in my paper on " *C.*" *australis* reasons were given for the view that the structures there referred to as aphlebiæ are merely the proximal homologues of pinnæ, and in the present paper also the two terms are employed somewhat indiscriminately.

As in the Australian zygopterid, the aphlebiæ are usually erect and repeatedly forked. The oval or elliptic cross-sections of their free lobes are seen in large numbers among the interstitial roots, in various stages of forking (Plate 49, fig. 3, Plate 50, figs. 5, 7). The ultimate segments are very fine, almost filiform. Figs. 12, 13, Plate 51, show the mode of attachment of three aphlebiæ ; one of the two seen in fig. 12 is coming off from the rachis almost horizontally, but this is the only instance of this kind so far observed. Figs. 5, 7 on Plate 2 show a number of free aphlebia-lobes ; some of them still lie in pairs formed by recent forkings, others are about to fork, as indicated by their paired vascular strands or by more or less obvious constrictions of their outline.

The *vascular supply to the appendages* arises in the form of closed rings nipped off, as in " *C.*" *australis* and *C. antiqua*, alternately from the two margins of the petiolar strand (Plate 50, fig. 9 ; Plate 51, fig. 15). But it is interesting to observe that the points of origin of these rings are not strictly the lateral, but the dorso-lateral, margins of the primary bundle—a fact which betrays the *Asterochlæna*-like behaviour of a petiolar strand otherwise typically clepsydroid. The outward course of the aphlebia-traces through the petiolar cortex is always dorso-lateral, as in " *C.*" *australis*, *Asterochlæna laxa*, and other zygopterids.

So far as I have seen, the aphlebia-trace never undergoes a dichotomy within the petiolar cortex, as it was observed to do in " C." *australis*. STENZEL mentions such a precocious dichotomy of the strand, leading to a " dineuroid " condition, like that figured in " C. " *australis*,‡ and he also figures the condition in one of the petioles§ ; but a comparison of the type-specimen does not confirm the accuracy of his figure, in other respects so faithful to the original. The aphlebia in our fig. 13, Plate 3,

* SCOTT (1920), p. 297, fig. 134 ; lobed or branched aphlebiæ are also well known to occur in *Botrychioxylon* (SCOTT, 1912*a*) and other zygopterids.

† SCOTT (1912), p. 51.

‡ SAHNI (1928), Plate 3, fig. 12 and text, pp. 16–17.

§ STENZEL (1889), p. 21, and Plate 4, fig. 38*b*.

appears to contain two strands, but the preservation is not clear enough to make this free from doubt, and I have not met with any other instance of the kind.

The *leaf-trace* reveals some points of considerable theoretical interest. Figs. 2, 8, 10, 11, 16–25 (from several different leaf-traces) show the earlier phases of the strand. The emission of a leaf-trace does not disturb the continuity of the xylem cylinder. The latter bulges out in front of one of the " pith "-rays, and from the end of the latter the single protoxylem of the incipient leaf-trace is derived by abstriction, in very much the same manner as in *Asterochlæna laxa*.* Shortly before the strand is to leave the stele the protoxylem is seen to be associated with an island of parenchyma. Whether this parenchyma has all appeared *de novo*, or whether the protoxylem originally brought with it a few thin-walled cells from the " pith "-ray, is difficult to ascertain. But by the time the leaf-trace becomes detached from the stele the island of parenchyma has again disappeared. At this stage (figs. 10, 16) the trace is of circular shape, with a mesarch, but eccentrically placed, protoxylem. The centrifugal xylem is better developed than the centripetal and, moreover, consists of tracheides of a distinctly larger size. The strand now closely resembles the corresponding stage in *Zalesskya gracilis* K. and G.-V.,† a Permian fern, probably of Osmundaceous affinities, also from Western Siberia. In this species, too, the single protoxylem is placed nearer to the adaxial margin of the leaf-trace, and the centrifugal tracheides are distinctly larger than the centripetal. The same feature is seen in *Z. uralica*, Zalessky,‡ another Permian species from the same region, which, as Prof. Zalessky says, is so similar to *Z. gracilis* that it may be identical with it. In the related forms *Thamnopteris schlechtendalii* Eichw. sp.§ and *T. kidstoni* Zalessky,‖ likewise from the Permian of Western Siberia, the protoxylem is again placed somewhat nearer to the adaxial side of the bundle, but the difference in size of the tracheides on the two sides, although unmistakably present, is less marked than in *Zalesskya*. The phylogenetic significance of these resemblances between *Asterochlænopsis* on the one hand and these Permian Osmundaceœ on the other is obvious.

It is noteworthy that at this stage the resemblance with *Asterochlæna* is not so close, for in this genus the protoxylem divides before the separation of the trace.¶ In the

* Bertrand (1911).

† Kidston and Gwynne-Vaughan (1908), Plate 3, figs. 14, 15*a*, 15*b*; Zalessky (1927), Plate 20, fig. 2.

‡ Zalessky (1924), p. 357; Zalessky (1927), Plate 20, fig. 8; possibly also in *Zalesskya diploxylon* (Zalessky, 1927, Plate 20, fig. 5).

§ Kidston and Gwynne-Vaughan (1909), Plate 4, fig. 18; Gwynne-Vaughan and Kidston (1908), p. 434, figs. 1–3.

‖ Zalessky (1924), p. 351, Plate 32, fig. 4; Zalessky (1927), Plate 21, fig. 3; possibly also in *Thamnopteris Gwynne-Vaughani*, Zalessky (1924, pp. 354–355).

¶ Bertrand (1911), p. 16. An approach to the condition in *Asterochlæna* is shown by some unusual leaf-traces found in *Thamnopteris schlechtendalii* by Kidston and Gwynne-Vaughan (1909, Plate 5, figs. 33–35), who compared them with *Clepsydropsis*. These authors as well as Prof. Paul Bertrand (1911, 1911*b*) have already drawn attention to the importance of these bipolar mesarch traces of *Thamnopteris* as an index of affinity between the Osmundaceæ and Zygopterideæ.

next stage the protoxylem has divided into two strands which lie in the tangential plane, temporarily connected together by a bridge of narrow tracheides. Even during this bi-polar stage the adaxial xylem may for a time be less developed and consist of narrower elements than the abaxial. This condition is clearly seen in the top right-hand leaf-trace in Plate 50, fig. 10, which should be compared with a bipolar leaf-trace of *Thamnopteris schlechtendalii* figured by KIDSTON and GWYNNE-VAUGHAN.* But very soon the protoxylems come to occupy a position which is symmetrical with regard to both the tangential and the radial planes (Plate 3, figs. 22, 23).

As the bundle steadily expands and assumes an elliptic form, each of the protoxylems develops into a peripheral loop (fig. 21), and for a time the strand closely recalls a stage hurried through by the leaf-trace of *Asterochlæna laxa*. But for the fact that the peripheral loops are permanently closed, the resemblance of this temporary phase with the definitive form of the petiolar strand of *Dineuron* would be extremely close. Presently the elliptic outline gives place to a distinctly fusiform shape (figs. 19, 24, 25), exactly like that of a diarch root-bundle of the same plant, although, of course, the immersed protoxylems leave no chance of confusion. This is about the level at which the relatively slender petiole becomes free from the stem. From this fusiform stage the definitive clepsydroid form is gradually moulded by a marked tangential stretching of the bundle, accompanied by a faint median constriction.

It is important to note that there is never the least sign of a curvature in the trace. In *Asterochlæna laxa* the fully formed bundle shows a slight adaxial curvature: in "*Clepsydropsis*" *australis*, as in *Ankyropteris*, one stage is abaxially curved; in *Asterochlænopsis* the strand remains perfectly straight throughout (text-fig. 4).

(iii) *The Root.*—The structure of the root (Plate 51, fig. 14) is not very well preserved, except for the diarch xylem, which is exactly of the same shape as in "*C.*" *australis*. The phloem, pericycle and endodermis can no longer be made out. The cortex is in three zones; the middle zone is dark and lies very near the periphery. Root-hairs have been made out only in one place, but the preservation, as stated, is poor.

The appearance of the dark middle zone of the cortex at first makes one suspect a mycorrhiza (I had suspicions of this even in "*C.*" *australis*), but I have not been able to detect any fungus or other organism in the poorly preserved tissues.

(iv) *Intrusions.*—The intrusive roots have already been mentioned; they recall the condition in "*C.*" *australis*. In the present case, however, they have only been seen in a few of the outermost petioles. They may have been commoner in leaves further out, which have been removed by decortication.

As in the case of "*C.*" *australis*, there is no reason to suppose that these intruded roots belong to any other plant than the one in which they are found. The conditions are very similar to those in the Australian plant. Here, too, the xylem is feebly developed, only the protoxylem being lignified, and the middle dark zone of the cortex is missing. In fig. 9, Plate 2, the two protoxylems have become displaced, owing to the

* KIDSTON and GWYNNE-VAUGHAN (1909), Plate 5, fig. 35.

disintegration of the delicate intervening tissue, the yet unlignified metaxylem. The same condition was frequently observed in the Australian plant.*

While describing "*C.*" *australis* I discussed in some detail the manner in which the intrusive roots had probably found their way into the petioles. It was suggested that the roots in the peripheral zone of the trunk, in their normal downward course, probably entered the open ends of decaying rachis-stumps; several such stumps were actually observed with numerous roots invading the crushed tissues within their sclerenchymatous sheaths. In the present case the material is not sufficient for such a detailed investigation of the phenomenon, but the conditions are so similar to those previously described that there seems no reason to doubt that here too the roots invaded the petioles in the same manner.

Genus *Asterochlænopsis* nov.

Tree-ferns allied to *Asterochlæna* and "*Clepsydropsis*" *australis*. Stem simple, with a central leaf-bearing axis surrounded by a thick zone of crowded erect persistent petioles, with interstitial roots, and possibly covered by a root-felt. Cauline stele more or less cylindrical, that is, devoid of arms; consisting of a thin xylem ring, enclosing a relatively large stellate "mixed pith"; "pith"-rays numerous. The leaf-trace at its origin has a mesarch protoxylem resembling that of *Zalesskya* and *Thamnopteris*, but in its subsequent phases recalls the condition in *Asterochlæna*, except that it never shows any curvature and retains a symmetry along two planes. Final form of petiolar trace as in the genus *Clepsydropsis* of UNGER. Pinna- or aphlebia-traces given off as closed rings alternately from the two sides of the petiolar strand, but from points slightly abaxially placed (a condition intermediate between *Clepsydropsis* and *Asterochlæna*). Aphlebiæ placed in two series, one on either side of the rachis, usually erect, repeatedly forked; ultimate segments filiform. Roots diarch, devoid of secondary xylem. Fertile organs unknown.

The only known species is

Asterochlænopsis kirgisica, STENZEL, sp.†

1889 *Asterochlæna* (*Clepsydropsis*) *kirgisica*, STENZEL, 'Die Gattung Tubicaulis,' p. 20, Plate 4, figs. 38–44.

1889 *Clepsydropsis kirgisica*, *ibid.*, p. 25.

1889 *Rachiopteris ludwigii*, LEUCK. and SCHENK, in SCHENK, 'Ueber Medullosa Cotta und Tubicaulis Cotta,' pp. 553–554, Plate 3, figs. 50, 51.

* SAHNI (1928), Plate 6, fig. 45. I am indebted to Dr. SCOTT for drawing my attention to the fact (which I had overlooked when writing on "*Clepsydropsis*" *australis*) that the rhizomes of *Asteroxylon* are frequently found intruded into other rhizomes of the same plant (KIDSTON and LANG, 1920, p. 645, and Plate 1, figs. 2–4).

† I am adopting the specific name *kirgisica* as being the better known of the two. As already stated there is no clear evidence on the question of priority. STENZEL'S specimen was also more complete than SCHENK'S, as it included the leaf-bearing axis.

1896 *Asterochlæna kirgisica*, STENZEL, 'Nachträgliche Bemerkungen zur Gattung Tubicaulis,' p. 29.

1909 *Clepsydropsis kirgisica* in PAUL BERTRAND, 'Etudes sur la fronde des Zygoptéridées,' p. 204.

1919 *Clepsydropsis kirgisica* in SAHNI, 'On an Australian specimen of Clepsydropsis,' p. 83.

Locality.—Near Pawlodar on the River Irtisch, between Akmolinsk and Semipalatinsk in the Kirgis Steppes, Ural (West Siberia). Not found *in situ*. For further details see GOEPPERT U. STENZEL, 1881, p. 126.

Age.—Unknown, possibly Permian.

Original Specimens and Sections.—(See text-figs. 1 and 2).

(1) STENZEL'S type-specimen "*Asterochlæna* (*Clepsydropsis*) *kirgisica*" (Mineralogical Museum, Dresden).

(2) SCHENK'S type-specimen "*Rachiopteris ludwigii*" (Botanisches Institut, University of Leipzig).

(3) LANGE'S specimen (Mineralogical Museum, Dresden).

(4) Specimen No. 96 of the Leuckart Collection (Städtisches Museum, Chemnitz).

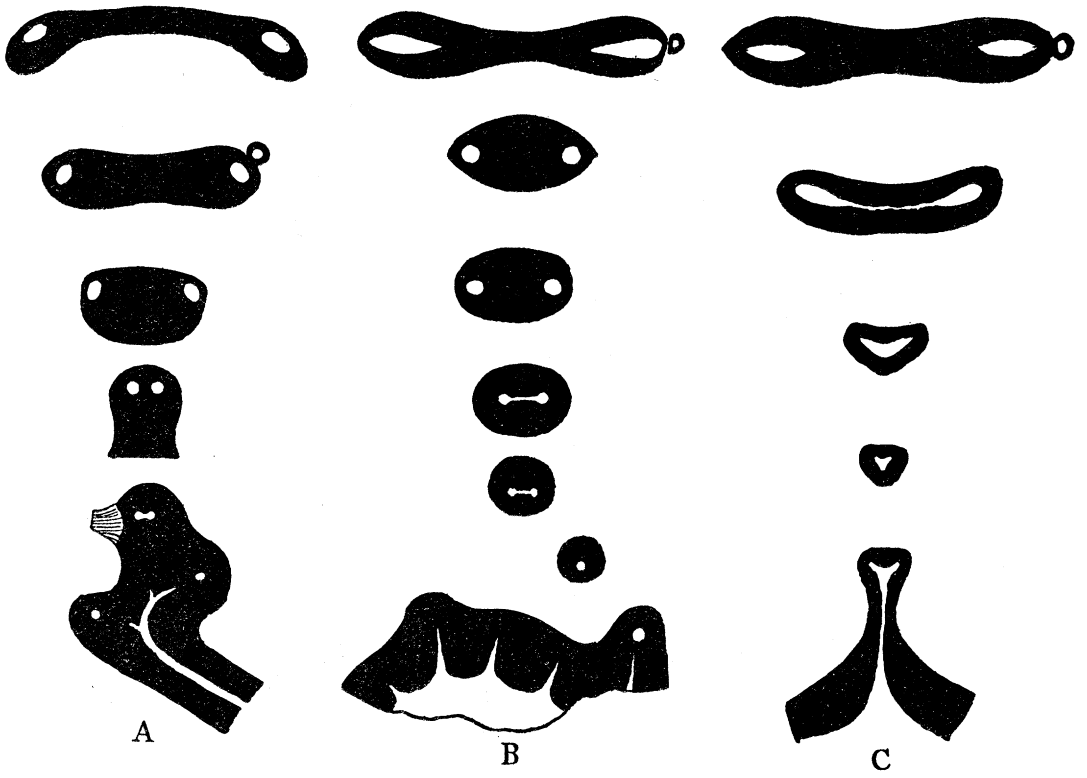
(5) GOEPPERT'S specimen (Geologisches Museum der Universität und Technischen Hochschule, Breslau).

Theoretical Considerations.

(*a*) *Affinities of Asterochlænopsis.*—From the foregoing description the affinities of the Siberian Zygopterid with *Asterochlæna* on the one hand and with the Australian Zygopterid on the other will have become apparent. But in spite of the clear resemblances with both these plants, it is evident, in view of the new facts brought to light, that it is generically distinct from either of them. The affinity with *Asterochlæna* is on the whole closer than with the Australian plant, in spite of the form of the petiolar bundle. *Asterochlænopsis* thus seems to be an appropriate name for the new genus.

In his memoir on *Asterochlæna laxa*, Prof. PAUL BERTRAND showed that the leaf-trace before assuming its definitive form passes through an uncurved clepsydroid stage. Even during this stage, however, the vascular strands for the appendages of the primary rachis (pinnæ or aphlebiæ) come off not from the extreme edge of the trace but from points somewhat abaxially placed. This transitory phase is therefore really more like the definitive form in *Asterochlænopsis* than like that in "*Clepsydropsis*" *australis* (text-fig. 4). In its earlier phases too the development of the leaf-trace in *Asterochlæna* runs parallel to that of the Siberian genus. But if we compare the parallel series of changes stage by stage, we notice that the whole development of the leaf-trace in *Asterochlæna* is, as it were, shifted one stage forward: the trace leaves the stele at the bipolar stage, that is, a stage later than in *Asterochlænopsis*, and the changes are continued a step beyond what we may call the *Asterochlænopsis*-stage. It is well known that a similar parallel progression is to be observed in other Zygopterideæ.

Recent work on the anatomy of ferns tends to show that the sequence of changes undergone by the leaf-trace has a phylogenetic significance. The most notable contributions to this principle are those by GWYNNE-VAUGHAN and KIDSTON,* by W. T. GORDON† and by PAUL BERTRAND.† The last-named author has ably summed up the facts and extended the application of the principle to the Zygopterideæ on the basis of his own unrivalled knowledge of this group. We are now accustomed to look upon the



TEXT-FIG. 4.—Diagrams to show the parallelism in the leaf-trace sequence in three allied genera of Zygopterideæ. A, *Asterochlæna* after BERTRAND; B, *Asterochlænopsis*; C, "*Clepsydropsis*" *australis*.

transient phases of the leaf-trace as recalling in a general way the fully developed bundles in a line of ancestral forms. Thus in the present case *Asterochlænopsis* would be regarded as belonging to a stock ancestral to *Asterochlæna*.

The affinity of the Siberian fern with "*Clepsydropsis*" *australis*, so forcibly expressed in the shape of the petiolar strand, is largely discounted by the leaf-trace characters, the crowded phyllotaxis and the simple stem organisation.

The stele, too, although it is only partially known, has more in common with that of *Asterochlæna*. The presence of a stellate "mixed pith" is common to the three forms, but the large number of rays ("protoxylem bands") with which the crowded

* GWYNNE-VAUGHAN and KIDSTON (1908), p. 435.

† GORDON (1911), p. 711; GORDON (1911*a*), p. 163.

‡ BERTRAND (1911); BERTRAND (1911*b*), pp. 213, 266–270. See also SAHNI (1923), pp. 209–212.

phyllotaxis goes hand in hand is a special feature of *Asterochlæna* and *Asterochlænopsis* not shared by any other known member of the family. If the stele of *Asterochlænopsis* were to become deeply invaginated here and there between the rays (at some points more deeply than at others) we should have a condition somewhat like a simplified *Asterochlæna* stele. Knowing the transformations which modern fern steles undergo during the ontogeny, it is not inconceivable or even improbable that the long spidery arms, so characteristic of the stele of *Asterochlæna*, were only an " adult " feature replacing a simpler, more or less cylindrical, condition in the juvenile state. It is by no means suggested that there is anything specially " juvenile " about the stele of *Asterochlænopsis*, but the structure of the stele, viewed comparatively, does seem to support the conclusion drawn from the facts of leaf-trace development.

I confess the idea did cross my mind that if the more distal parts of the stem and leaf were available the Kirgis plant might show itself to be in reality an *Asterochlæna*: that, if traced distally, the stele would begin to develop spidery arms over the protoxylem bands, and the petiolar strands tend to show an Asterochlænoid curvature. But at least so far as the foliar bundles are concerned I have reason to believe that their actual form may safely be taken as the definitive one.* By calculating the rate at which an average petiole diverges from the vertical axis† I have found that it requires a length of at least 18 cm. to pass from the inner edge of the peripheral zone, where the clepsydroid form has already been acquired, to the outermost edge of the fossil. During this very considerable distance there is no sign of an adaxial curve, and it is highly improbable that one will develop higher up. *Asterochlænopsis* thus seems to be a definitive type and not a stage in the ontogeny of an *Asterochlæna*, although we should probably be justified in regarding it as belonging to, or related to, the parent stock of that genus.

It may be that if we knew more about the phyllotaxis of the Siberian plant we could bring it into closer relation with the Australian form. Probably, if we could telescope into a short distance a long relatively lax-leaved stem, such as that of *Ankyropteris scandens*, or one of the individual axes composing the false stem of " *Clepsydropsis* " *australis*, we should obtain not only the crowded leaf-arrangement seen in *Asterochlænopsis*, but also the supernumerary " pith "-rays. But with the small fragment of the stele available any attempt to ascertain the phyllotaxis seems hopeless.

Another interesting fact about the leaf-trace sequence in the Kirgis fossil is the close resemblance shown by the earliest stages with the corresponding parts in *Zalesskya* and *Thamnopteris*. It will be remembered that it was in *Thamnopteris schlechtendalii*

* For a similar reason I think the characteristic form of the strand in "*Clepsydropsis*" *australis* may also be regarded as the " permanent " one. Unfortunately it is only rarely that zygopterid petioles are preserved in sufficient lengths to leave us without a feeling of insecurity on this point, which so closely touches our specific and even generic distinctions. I am here, of course, leaving out of consideration the inevitable and profound alterations which the rachis-strand must undergo in the region beyond the petiole.

† This is about 7·5 mm. in a vertical height of 46 mm., which gives an angle of about 9° with the vertical.

that KIDSTON and GWYNNE-VAUGHAN* first discovered indications of affinity between the Osmundaceæ and the Zygopterideæ. At its point of origin the leaf-trace of *Thamnopteris* is circular or elliptic in section, with generally a single almost central protoxylem, but sometimes the protoxylem has already bifurcated in the tangential plane. To this mesarch bipolar bundle a good deal of importance has been attached, owing to the occurrence of a similar bundle, also as a transient phase, in many Zygopterideæ. The leaf-trace of *Asterochlænopsis* not only passes through this stage, but it also arises in the unipolar condition which is normal for *Thamnopteris* and *Zalesskya*. The fact that all the three genera are confined to Western Siberia lends force to these resemblances, and may strengthen the presumption that *Asterochlænopsis* like *Thamnopteris* and *Zalesskya* was of Permian age.

The reduction in the adaxial xylem, to which attention has already been drawn, is intelligible as an expression of a wide-spread tendency among ferns to acquire a C-shaped leaf-trace (GWYNNE-VAUGHAN and KIDSTON). But the *temporary* appearance of this feature in a Zygopterid fern (*e.g.*, *Asterochlænopsis*) where subsequently the adaxial xylem attains the same development as the abaxial, is of particular interest as a case of recapitulation. For it shows the development of an organ making a detour in its course, which can only be explained on the analogy of erratic behaviour in conscious beings under the influence of habit or memory.

Both on the strength of these resemblances and of the less striking ones in the stem stele, which have already been pointed out, the origin of the Zygopterideæ as a side line of evolution from the base of the main Osmundaceous stock seems a well founded conclusion.

(*b*) *The "stem of Clepsydropsis."*—The fact that in the Siberian and the Australian zygopterids petioles of the same *Clepsydropsis* type have been found attached to stems of two generically distinct plants reveals a rather interesting situation. It is well known that the genus *Clepsydropsis*† was founded on fragmentary rachises, presumed to be those of ferns, but that concerning their parent stem there has been a good deal of speculation. Prof. PAUL BERTRAND, who first suggested that the rachises are Zygopteridean,‡ once believed that the associated axes named *Cladoxylon* were the parent stems in question,§ but he later withdrew this opinion.‖ Soon afterwards, when Mrs. E. M. OSBORN¶ announced the discovery of the Australian Zygopterid, with *Clepsydropsis*-like petioles attached to stems having the *Ankyropteris grayi* type of stele, it seemed as if the stem of *Clepsydropsis* had at last been found. *Relying solely upon the similarity in the foliar bundle*, I concluded that UNGER's *Clepsydropsis* must have been borne upon the same kind of stem as the Australian plant; the latter was accordingly assigned to

* KIDSTON and GWYNNE-VAUGHAN (1910), 'Fossil Osmundaceæ,' Part 4, p. 469.

† UNGER (1856), p. 165.

‡ BERTRAND (1909).

§ BERTRAND (1908); (1911*b*), p. 250; (1911*c*).

‖ BERTRAND (1913), pp. 918–919; see also SOLMS-LAUBACH (1910), pp. 540–541.

¶ OSBORN (1915), pp. 727–728.

UNGER'S genus.* This step seemed quite natural at the time, and no one, so far as I know, has ever questioned it. But, as we have now discovered, *the clepsydroid strand is by itself no index of affinity.*† Till now we were accustomed to believe that in the Zygopterideæ the petiolar trace was a reliable generic character, and so it probably is, in most cases, but at least in the present instance we have been misled. *It now seems doubtful whether the rachises described by* UNGER *had anything more to do with the Australian Zygopterid than they have with the Siberian.*

A fresh inspection of UNGER'S material‡ has yielded no further clue as to the stem on which the rachises were borne, but it strengthens the suspicion that UNGER'S *Clepsydropsis* was generically distinct from any Zygopterids at present known. There are indications that the very slender axes containing diminutive clepsydroid strands, which Prof. BERTRAND described as *C. antiqua* var. *exigua*, are not the primary rachises of a variety of *C. antiqua* but *branch-rachises of a higher order, belonging to the same plant.*§ If these thin axes really are secondary or tertiary rachises of *C. antiqua* fronds (and UNGER'S Plate 7, fig. 17, actually shows such a branched leaf) the plant must have differed considerably not only from *Asterochlœnopsis* and from the supposed "*Clepsydropsis*" from Australia, but from all known Zygopterideæ.

In the circumstances, the safest course would have been to restrict the name *Clepsydropsis* to leaf-axes of unknown attribution, and to place the Australian plant, like the Siberian, in a new genus. Such a step would be compatible with the peculiar combination of characters shown by this geographically isolated member of the family. For the present, however, my intention is not to propose a new genus for "*Clepsydropsis*" *australis*, but to record my suspicion that this Carboniferous Zygopterid from the southern hemisphere has no special affinity with UNGER'S Devonian genus from Thuringia.

Thus the old problem concerning the "stem of *Clepsydropsis*" stands where it was; if anything, the question is more difficult than ever, for the affinities of *Clepsydropsis* with the Zygopterideæ are again thrown into doubt.

* SAHNI (1918), p. 375; (1919). I had even suggested on this ground a merging of the genus *Ankyropteris* in *Clepsydropsis*. On account of the difference in petiolar structure Dr. SCOTT (1920), p. 306, preferred to keep up both genera; and this was fortunate, for a combination would only have been a source of further confusion. I am now fully converted to Dr. SCOTT'S position.

† Clepsydroid bundles of a modifiedt ype are also found in *Asteropteris* (DAWSON, 1881, p. 299, BERTRAND, 1913).

‡ I owe a special debt of gratitude to Prof. GOTHAN, of the Prussian Geological Survey, for permission to borrow several of UNGER'S specimens and to cut fresh sections from them.

§ The possibility is not excluded that Unger's *Clepsydropsis* rachises, with their varying diameters, represented branches of a large *Hierogramma* frond, in which case a Thuringian *Cladoxylon* would still be the parent stem of *Clepsydropsis*. We must here exclude from consideration the Elberfeld species "*Cladoxylon*" *scoparium*, Kräusel & Weyland (1926), whose reference to *Cladoxylon* seems to me to be very doubtful, and which probably represents a new and distinct genus. There is no evidence that Unger's *Cladoxylon* branched in the manner of the Elberfeld species, or that it bore the aphlebioid leaflets and sporangierous shoot-systems so characteristic of the latter.

Summary.

The new genus *Asterochlænopsis* is founded on a well known silicified stem, picked up about 50 years ago near Pawlodar, in the Kirgis Steppes, Western Siberia. The original fossil having been cut into several pieces, two of these were described independently and almost simultaneously (1889) by STENZEL and by A. SCHENK respectively, under the names *Asterochlæna* (*Clepsydropsis*) *kirgisica* and *Rachiopteris ludwigii*. The identity of these species with each other, and the fact that the two type-specimens are fragments of one and the same stem, were suspected by the present author in 1919 and have now been proved by a comparison of the type-specimens, which have been found to fit together. At the same time other fragments of the original fossil have been brought together and several of the pieces have been examined for the first time in thin sections. This re-investigation has yielded the rather unexpected result that the fossil combines in itself the *Clepsydropsis*-like petiolar strand with a leaf-trace sequence resembling that of *Asterochlæna*, while the stem stele, hitherto practically unknown, is of a new type somewhat intermediate between those of *Asterochlæna* and *Ankyropteris*. In the structure of the leaf-trace at its point of origin there is a close resemblance with the Osmundaceous ferns *Zalesskya* and *Thamnopteris*, from the Permian of Western Siberia.

Asterochlænopsis thus constitutes, on the one hand, an interesting link between *Asterochlæna* and *Ankyropteris*, and, on the other, an additional piece of evidence for a common origin of the Zygopterideæ and Osmundaceæ.

A further result of the present investigation touches the question of nomenclature and classification in the Zygopterideæ. Some years ago, it was shown that two such distinct types of petiole as those of "*Clepsydropsis*" *australis* and *Ankyropteris grayi* may be borne upon stems having an almost identical type of stele. And now we learn that two petioles, so closely similar as those of "*Clepsydropsis*" *australis* and the Siberian plant (hitherto regarded as a species of *Clepsydropsis*) actually belong to two generally distinct types of stem. Facts of this kind are a forcible reminder that however useful leaf characters may be in the classification of this family, they may sometimes be very misleading.

The discovery that rachises with typical "*Clepsydropsis*" bundles may be borne upon such different kinds of stems throws into suspicion the affinities of the fragmentary remains on which the genus *Clepsydropsis* was founded by UNGER. A revision of part of the material originally described by UNGER, and later by others, seems to indicate that UNGER'S *Clepsydropsis* belonged to a plant which was generically distinct from both the Siberian and the Australian Zygopterids, and was possibly not a Zygopterid at all. In spite of their "*Clepsydropsis*" petioles, the claim of these two ferns to that generic name is thus seriously in question. One of them has now been transferred to the new genus *Asterochlænopsis*; the other is being retained only very provisionally in UNGER'S genus.

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EXPLANATION OF PLATES 49–51.

Note.—*app.*, appendages of petiole (pinnæ or ? aphlebiæ); *app. tr.*, vascular supply of appendages; *i.r.*, intrusive root; *i.c.*, *m.c.*, *o.c.*, inner, middle, outer cortex; *i.l.t.*, incipient leaf-trace; *l.t.*, leaf-trace; *m.p.*, "mixed pith"; *p.r.*, "pith" ray; *pr.*, protoxylem; *r.*, root; *r.st.*, root stele; *st.*, stem stele; *x.c.*, xylem cylinder.

(Figs. 2, 3, 10, 21 and 23 are from photographs by Mr. W. TAMS; the rest are by the author.)

PLATE 49.

(All the figures are from untouched photographs.)

FIG. 1.—LANGE'S specimen, section at 13 mm. A sector of the stem, with several decurrent leaf-bases containing leaf-traces at different stages, is seen at the lower corner. The arrow indicates a fragment of the stele preserved at the edge of the section (*cf.* fig. 2). The roots in the vicinity of the stem are mostly running outwards, those in the dark peripheral zone are more often vertical. Mineralog. Mus. Dresden. Nat. size.

FIG. 2.—Part of the above section. * * outline of stem epidermis, including the decurrent leaf-bases. The stele shows an incipient leaf-trace with a central protoxylem; to the left of the stele is part of another leaf-trace. × 4.

FIG. 3.—Chemnitz specimen, section from the lower end (*cf.* text-fig. 1 E, Plate 50, fig. 10, and Plate 51, fig. 11). Städtisches Mus. Chemnitz. × 2.

PLATE 50.

(All the figures are from untouched photographs.)

FIG. 4.—STENZEL'S type-specimen, partial section at 22 mm. The adaxial side is towards the narrow left-hand corner of the figure. Mineralog. Mus. Dresden. Nat. size.

FIG. 5.—Part of the above section, showing the matrix of roots and aphlebiæ between the petioles. The adaxial side is towards the lower right-hand corner of the figure. Some of the aphlebia lobes are lying in pairs, being the result of recent dichotomy. The inset figure (from the same section) shows two aphlebiæ preparing to fork. × 5·5.

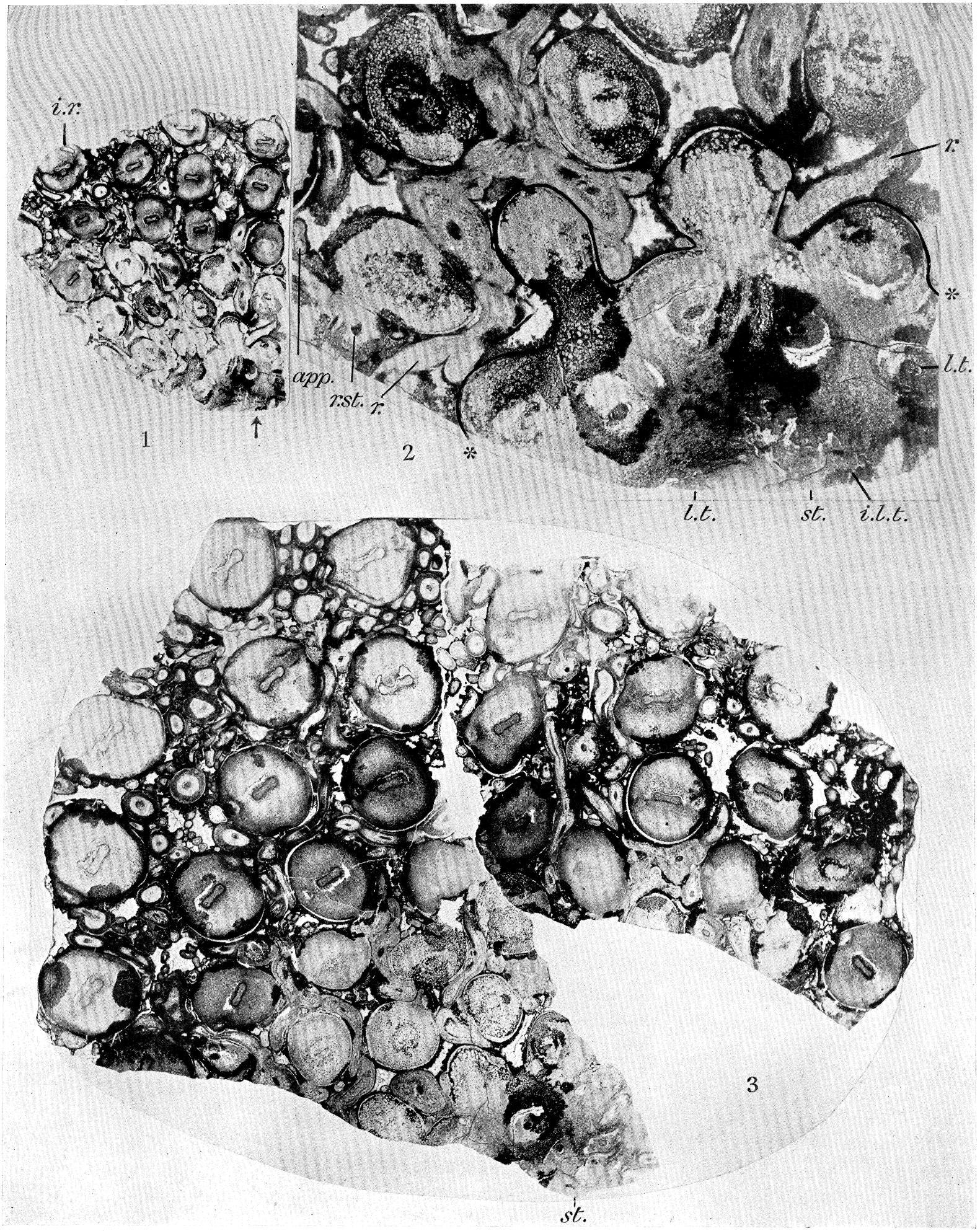
FIG. 6.—Part of the same section (the right-hand petiole in fig. 5). × *ca.* 16.

FIG. 7.—Part of the same section (*cf.* lower left-hand part of fig. 5) showing a group of aphlebiæ and a small root (with a well-developed diarch stele). The aphlebia in the top left-hand corner has a pair of strands. × *ca.* 14.

FIG. 8.—LANGE'S specimen, section at 7 mm. One of the three leaf-traces shows the protoxylems still connected by a bridge of narrow tracheids (*cf.* Plate 3, figs. 22–23). The adaxial side is turned downwards. Mineralog. Mus. Dresden. × *ca.* 6·5.

FIG. 9.—LANGE'S specimen, section at 13 mm., showing an early stage in the formation of a pinna (or ? aphlebia) trace. On the right an intrusive root of which the stele shows only the two protoxylems, the intervening metaxylem, not yet lignified, having decayed. This mode of preservation is identical with that seen in the intrusive roots of "*Clepsydropsis*" *australis*. This petiole is seen nat. size at the top right-hand corner of Plate 49, fig. 1. Mineralog. Mus. Dresden. × *ca.* 20.

FIG. 10.—Chemnitz specimen, section from the lower end, showing details of stem stele and leaf-traces. The numerals 1–5 are placed opposite to the "pith"-rays. Two incipient leaf-traces are seen at 2 and 5, the latter with a central cavity presumably once occupied by a tissue similar to the "pith." The free leaf-trace on the left has only one protoxylem, that on the right has two; in both the adaxial xylem is less developed than the abaxial (*cf. Zalesskya* and *Thamnopteris*). Städt. Mus. Chemnitz. × *ca.* 14.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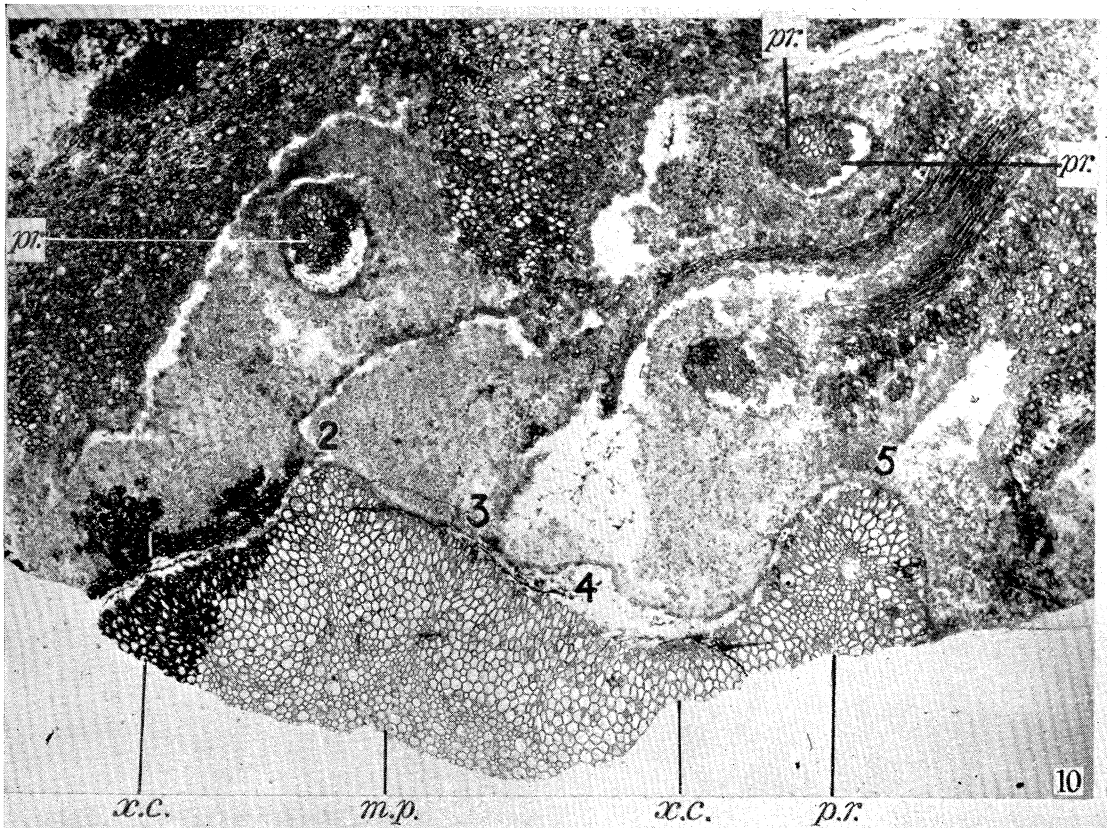
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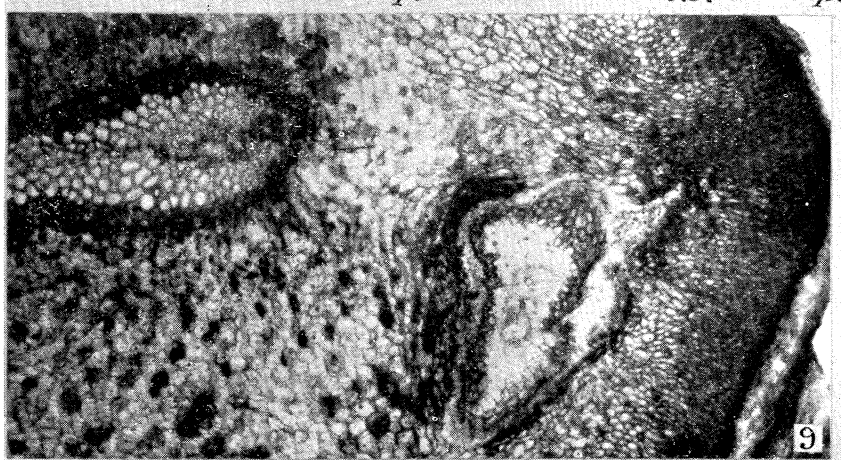
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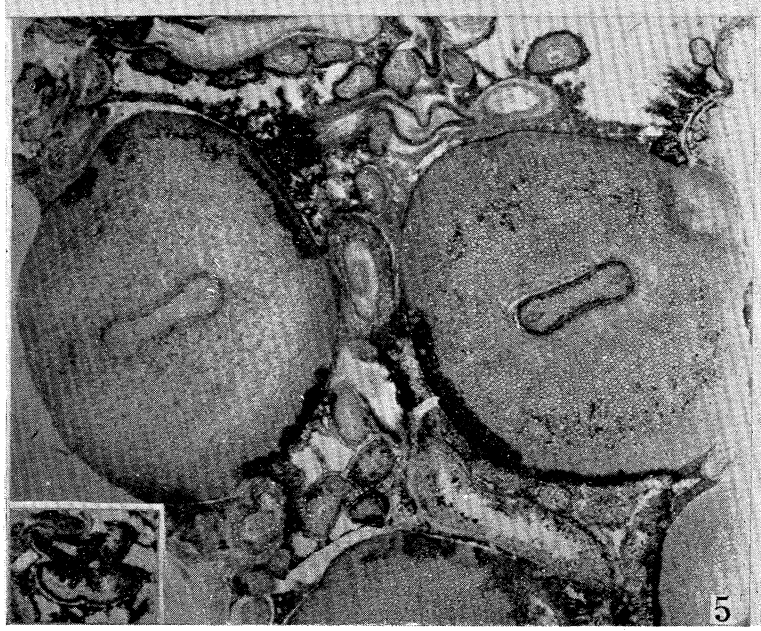
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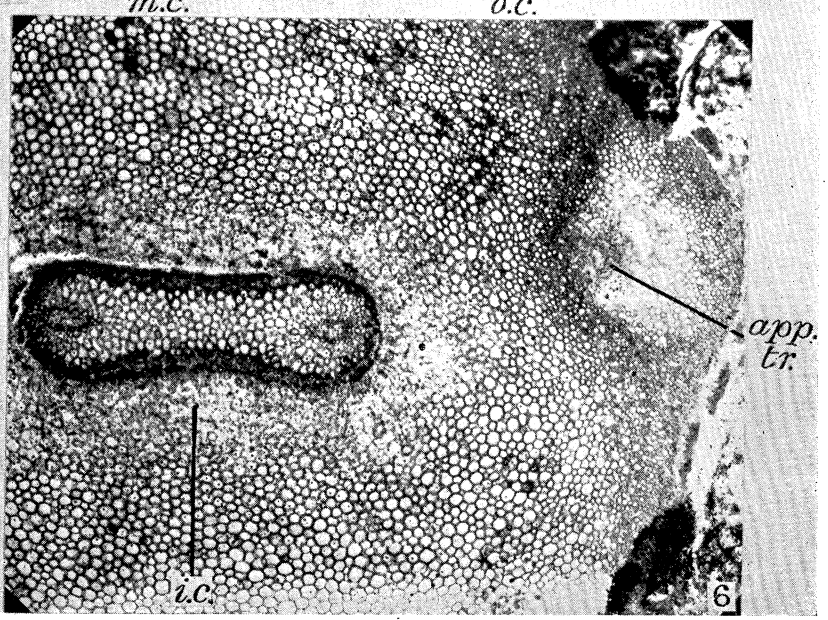
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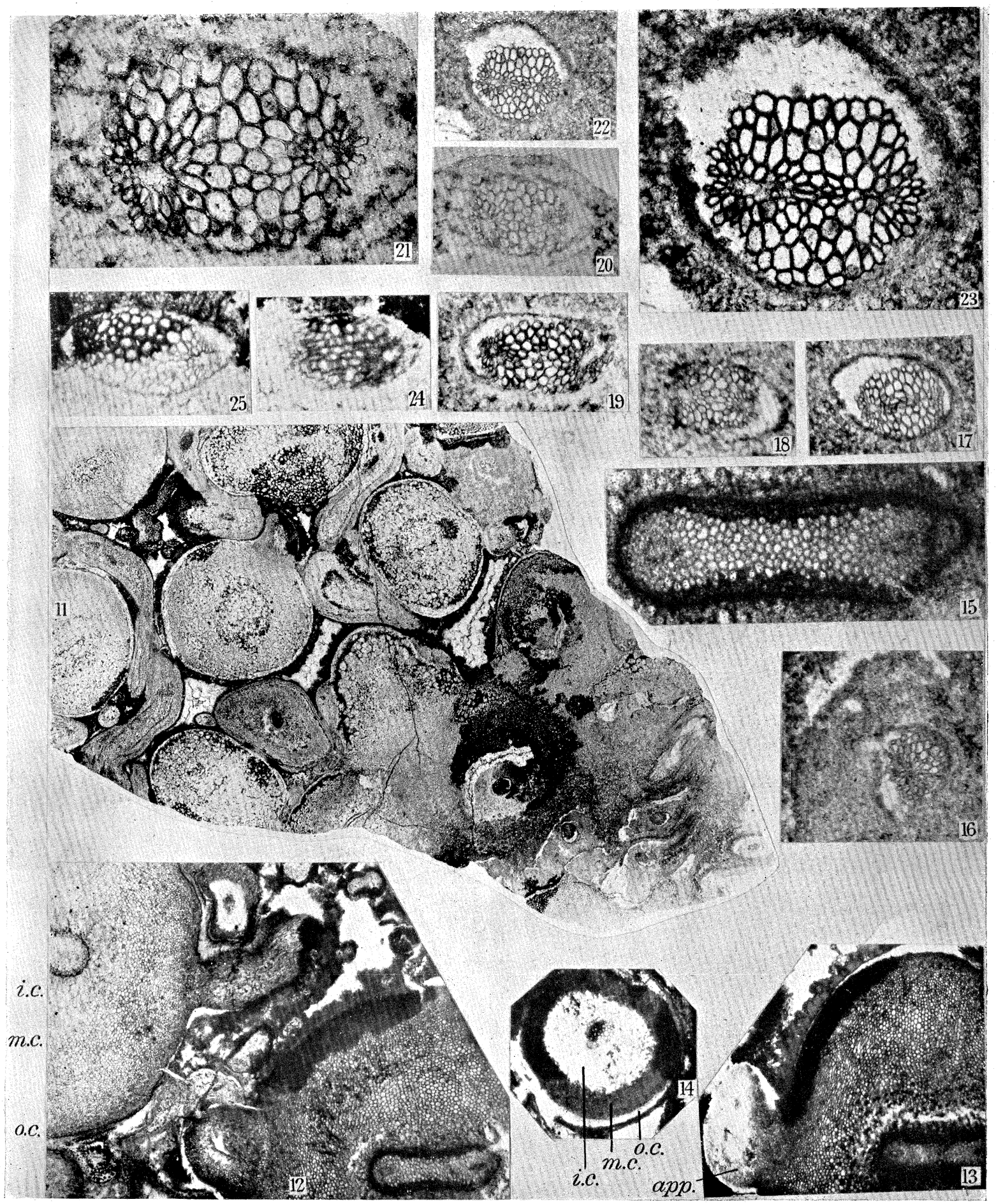
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Plate 51.

(All the figures are from untouched photographs.)

Fig. 11.—Chemnitz specimen, part of the same section (*cf.* Plate 49, fig. 3). Städt. Mus. Chemnitz. × 4.

Fig. 12.—Lange's specimen, section at 7 mm., showing the lateral appendages (? pinnæ or aphlebiæ) attached to two petioles. The appendage of the upper petiole is coming off at right angles to the leaf axis, that of the other seems to lie parallel to it. The latter petiole is seen cut 3 mm. higher up in fig. 15 ; and in that section there is no sign of this appendage, but the petiolar bundle is giving off a trace to an appendage on the opposite side. Mineralog. Mus. Dresden. × *ca.* 9.

Fig. 13.—Lange's specimen, section at 7 mm., the appendage seems to contain a pair of strands, but the preservation is too poor to show this for certain. Mineralog. Mus. Dresden. × *ca.* 9.

Fig. 14.—Lange's specimen, section at 13 mm., showing the structure of a root. × *ca.* 8·5.

Fig. 15.—Lange's specimen, section at 10 mm., showing the origin of a pinna- (or ? aphlebia-) trace from a point slightly abaxial to the actual margin of the petiolar trace. The same petiole is seen cut 3 mm. lower down in fig. 12. Mineralog. Mus. Dresden. × *ca.* 23.

Fig. 16.—Lange's specimen, section at 10 mm. A leaf-trace near its point of origin, already surrounded by its own cortex. The single protoxylem is nearer to the adaxial than to the abaxial margin (*cf.* fig. 10). Mineralog. Mus. Dresden. × *ca.* 25.

Figs. 17–20.—Lange's specimen. Several bipolar leaf-traces from the same section (10 mm.). In fig. 19 one of the peripheral loops is damaged ; in fig. 17 one of the loops appears not yet to have been formed. In all the figures the adaxial side is turned downwards. All × *ca.* 25.

Fig. 21.—The same leaf-trace as in fig. 20. × *ca.* 65.

Fig. 22.—Lange's specimen, section at 7 mm. A well-preserved leaf-trace with the peripheral loops joined by a bridge of small tracheides (*cf.* Plate 50, fig. 8). Mineralog. Mus. Dresden. × *ca.* 25.

Fig. 23.—The same leaf-trace. × *ca.* 65.

Figs. 24, 25.—Lange's specimen, section at 7 mm. Two fusiform leaf-traces (*cf.* Plate 2, fig. 8). Mineralog. Mus. Dresden. × *ca.* 25.

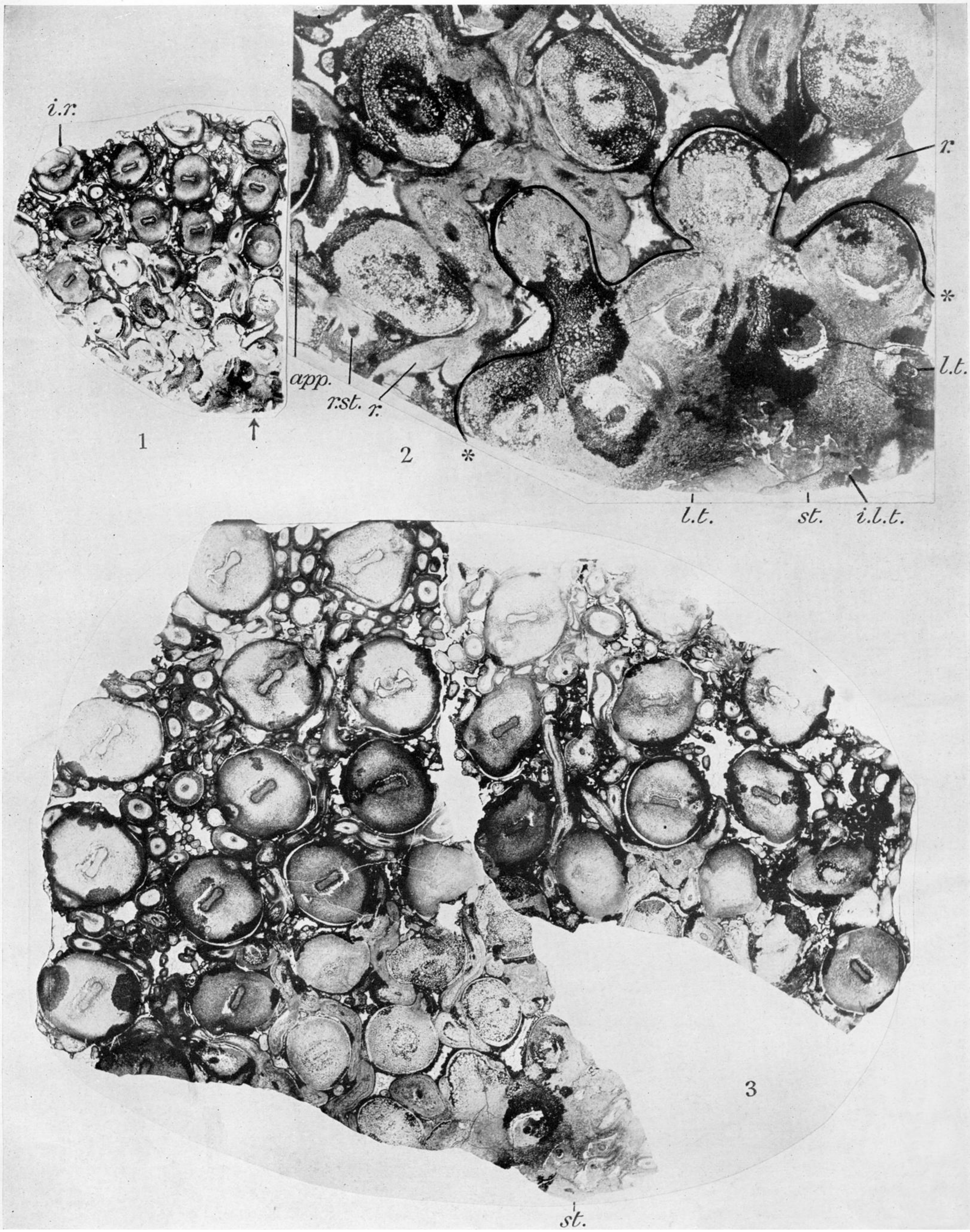


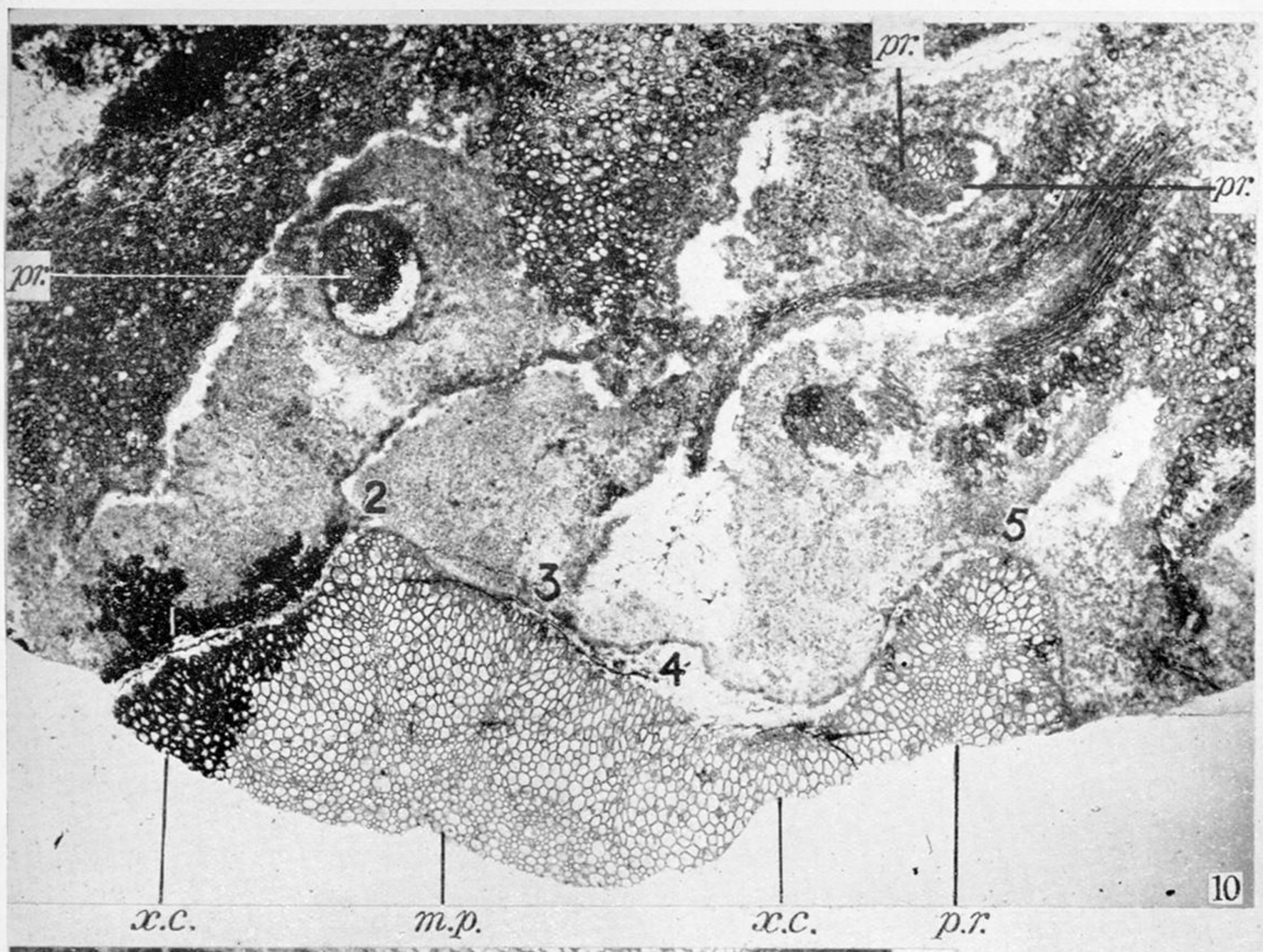
PLATE 49.

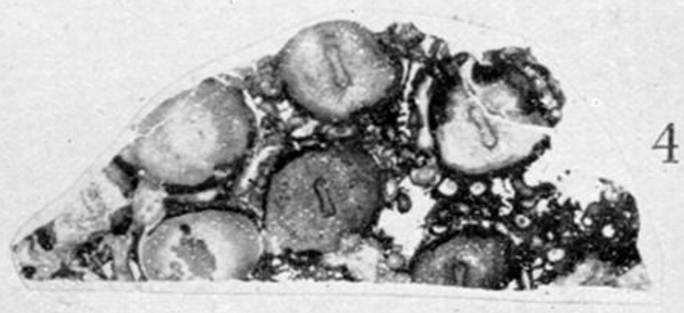
(All the figures are from untouched photographs.)

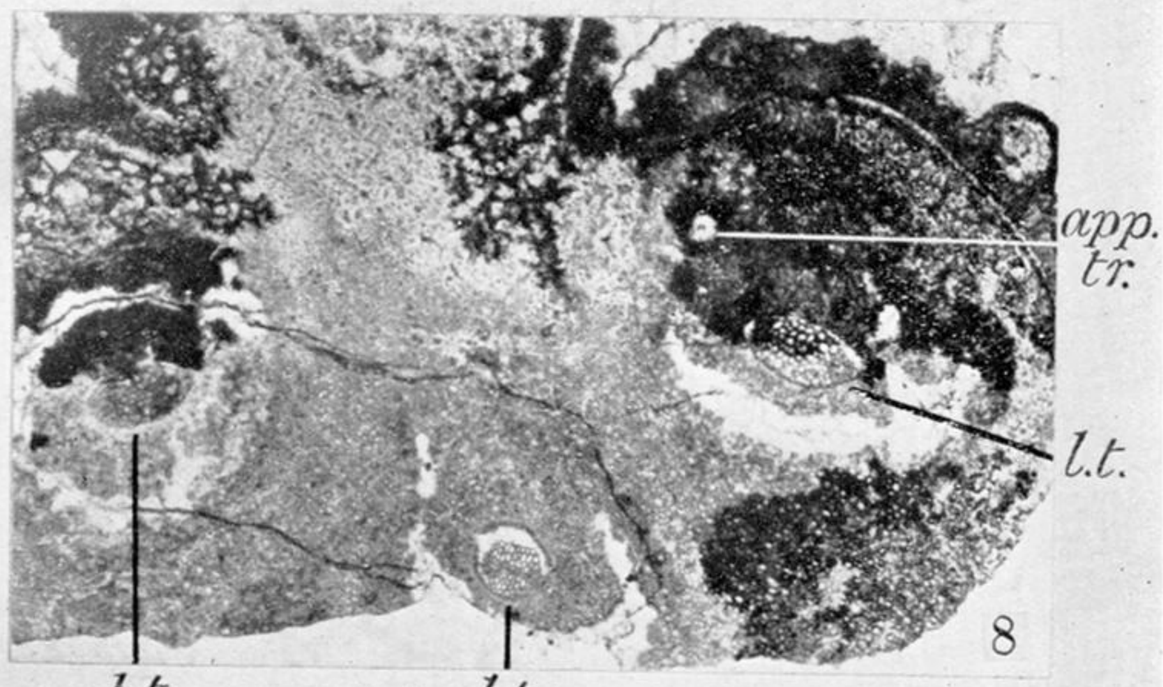
FIG. 1.—LANGE'S specimen, section at 13 mm. A sector of the stem, with several decurrent leaf-bases containing leaf-traces at different stages, is seen at the lower corner. The arrow indicates a fragment of the stele preserved at the edge of the section (*cf.* fig. 2). The roots in the vicinity of the stem are mostly running outwards, those in the dark peripheral zone are more often vertical. Mineralog. Mus. Dresden. Nat. size.

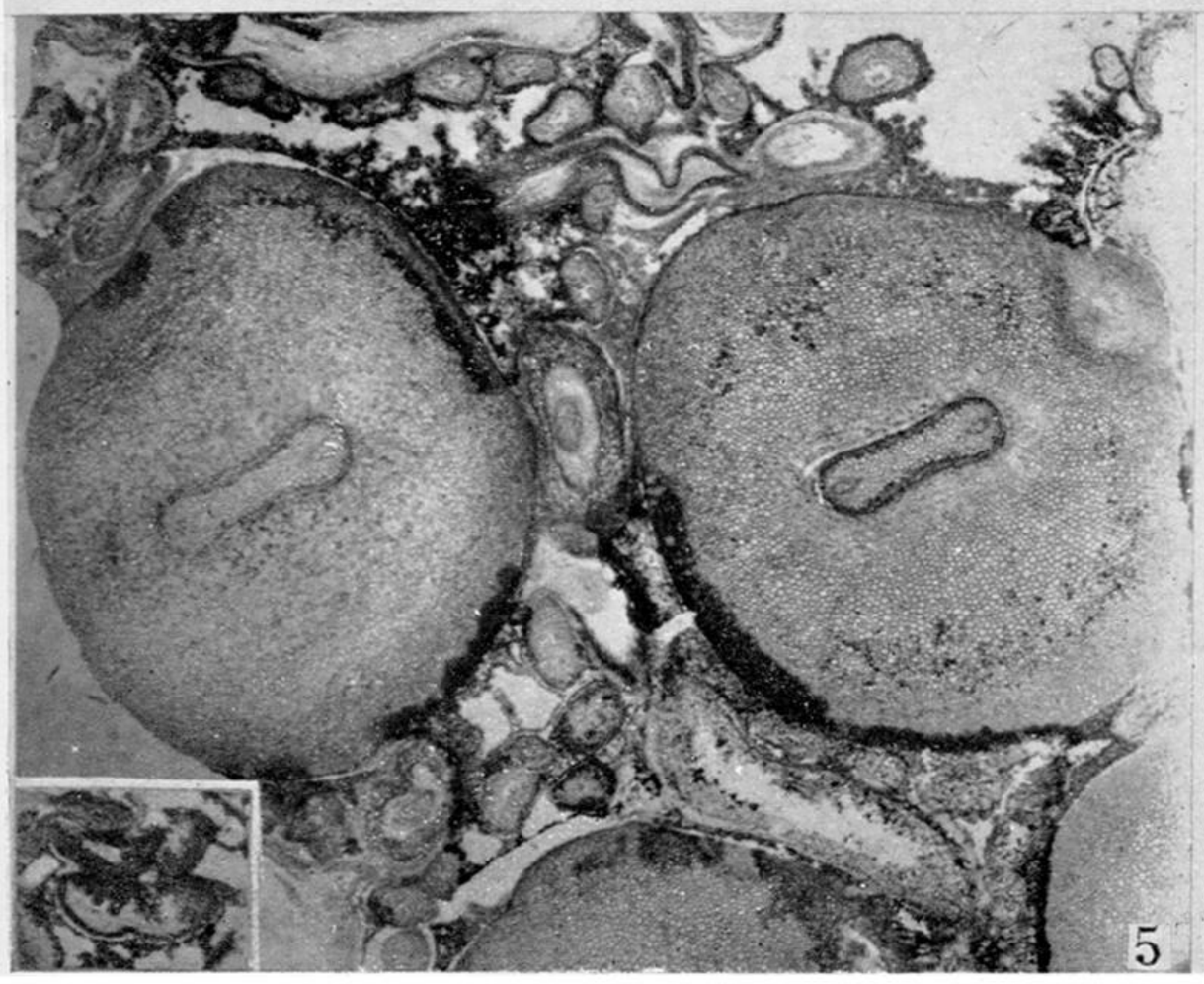
FIG. 2.—Part of the above section. * * outline of stem epidermis, including the decurrent leaf-bases. The stele shows an incipient leaf-trace with a central protoxylem; to the left of the stele is part of another leaf-trace. × 4.

FIG. 3.—Chemnitz specimen, section from the lower end (*cf.* text-fig. 1 E, Plate 50, fig. 10, and Plate 51, fig. 11). Städtisches Mus. Chemnitz. × 2.









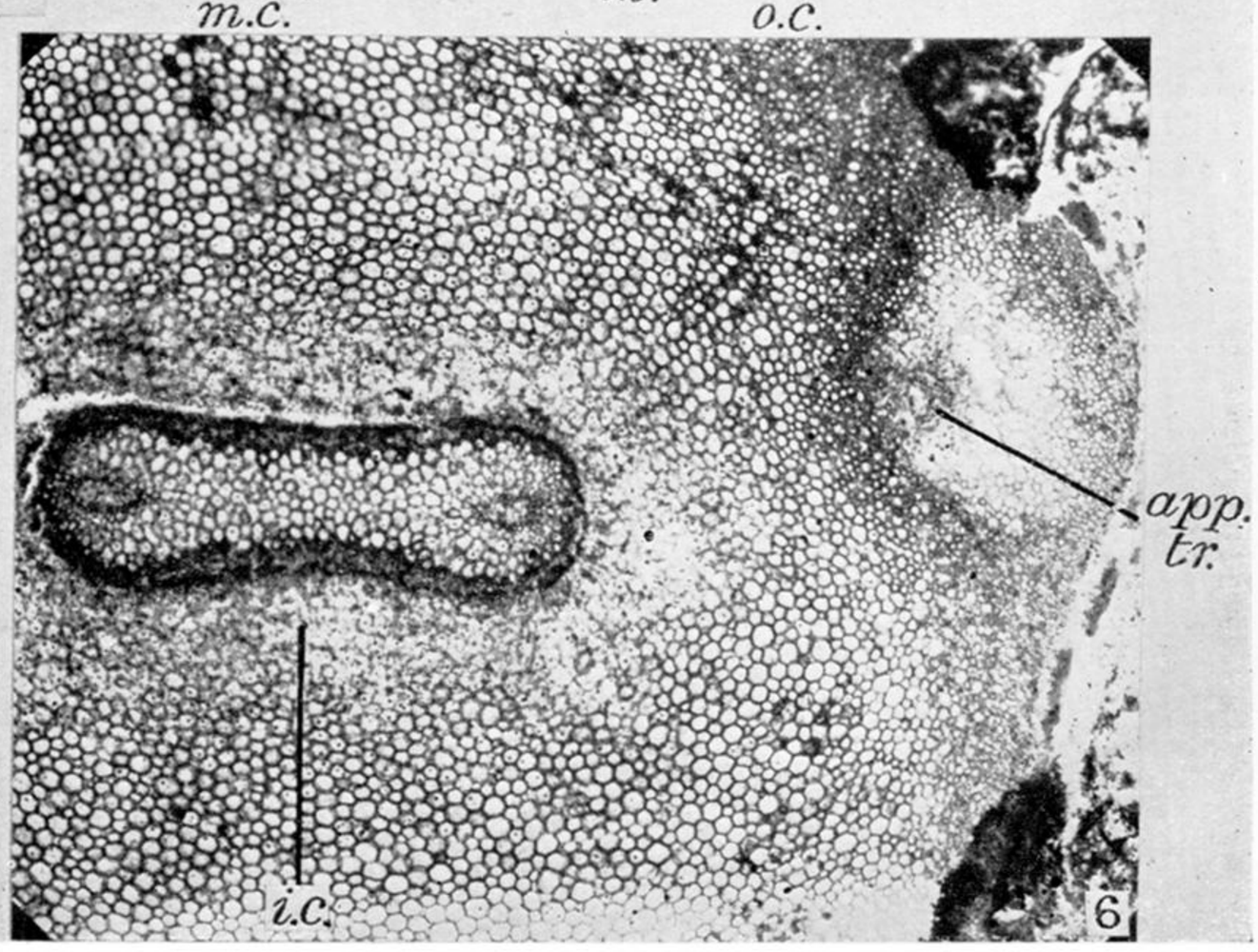


PLATE 50.

(All the figures are from untouched photographs.)

FIG. 4.—STENZEL'S type-specimen, partial section at 22 mm. The adaxial side is towards the narrow left-hand corner of the figure. Mineralog. Mus. Dresden. Nat. size.

FIG. 5.—Part of the above section, showing the matrix of roots and aphlebiæ between the petioles. The adaxial side is towards the lower right-hand corner of the figure. Some of the aphlebia lobes are lying in pairs, being the result of recent dichotomy. The inset figure (from the same section) shows two aphlebiæ preparing to fork. × 5·5.

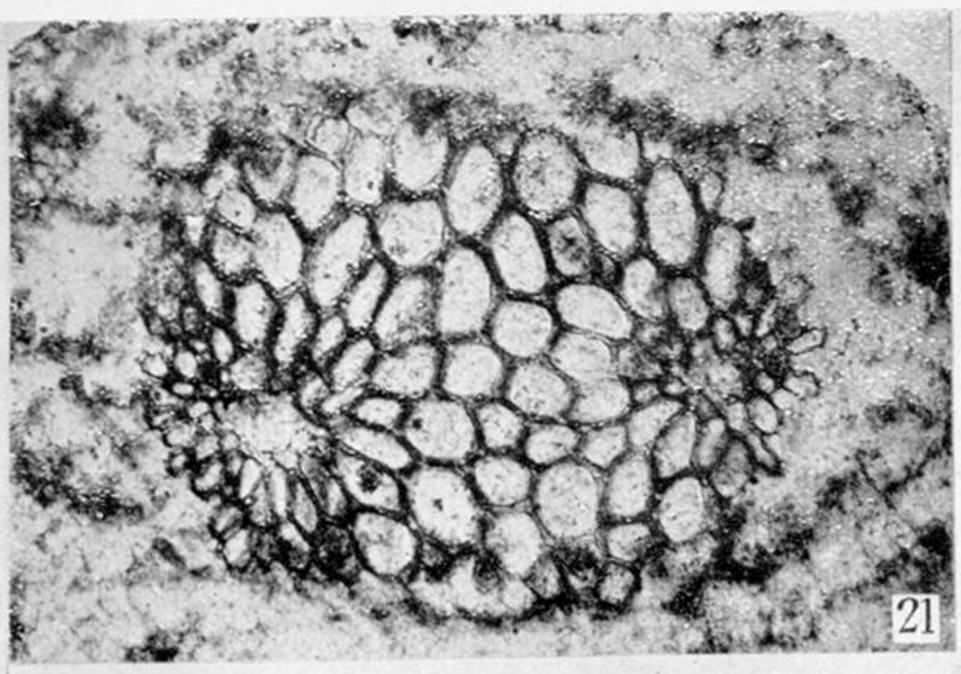
FIG. 6.—Part of the same section (the right-hand petiole in fig. 5). × *ca.* 16.

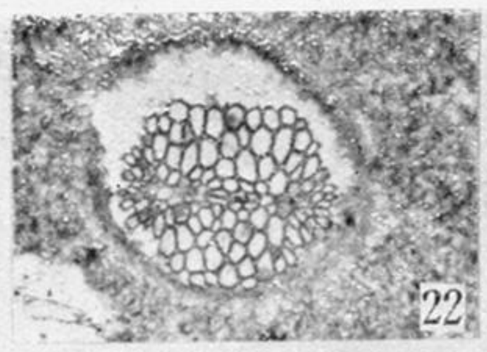
FIG. 7.—Part of the same section (*cf.* lower left-hand part of fig. 5) showing a group of aphlebiæ and a small root (with a well-developed diarch stele). The aphlebia in the top left-hand corner has a pair of strands. × *ca.* 14.

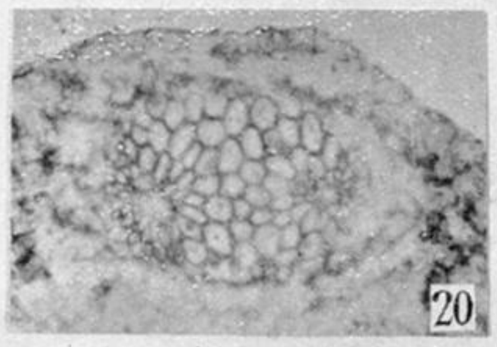
FIG. 8.—LANGE'S specimen, section at 7 mm. One of the three leaf-traces shows the protoxylems still connected by a bridge of narrow tracheids (*cf.* Plate 3, figs. 22–23). The adaxial side is turned downwards. Mineralog. Mus. Dresden. × *ca.* 6·5.

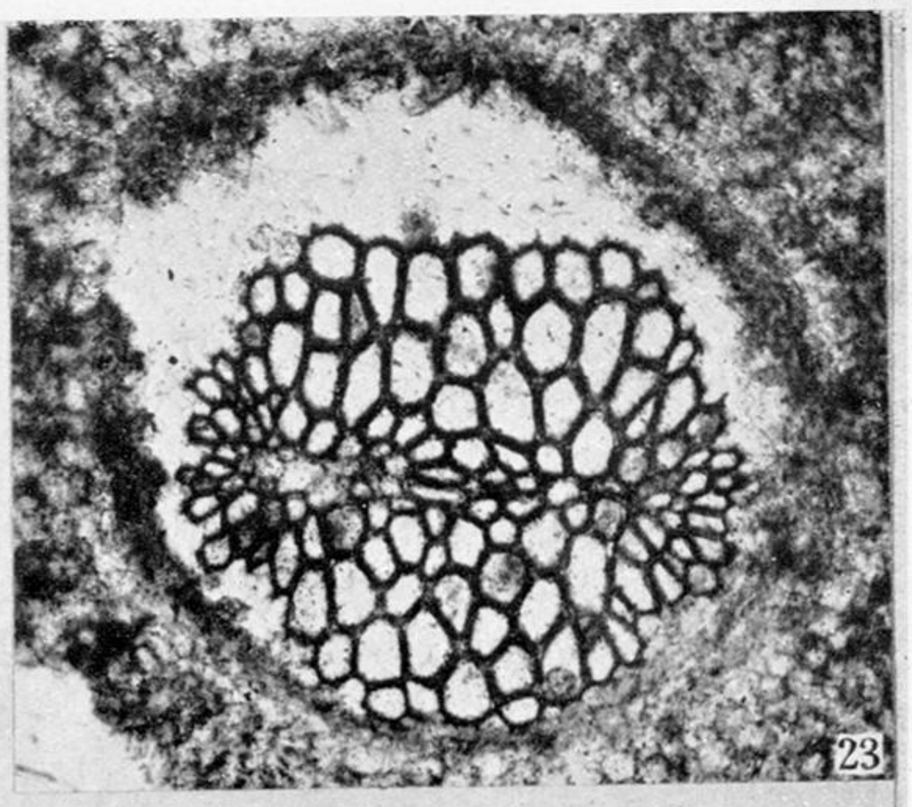
FIG. 9.—LANGE'S specimen, section at 13 mm., showing an early stage in the formation of a pinna (or ? aphlebia) trace. On the right an intrusive root of which the stele shows only the two protoxylems, the intervening metaxylem, not yet lignified, having decayed. This mode of preservation is identical with that seen in the intrusive roots of "*Clepsydropsis*" *australis*. This petiole is seen nat. size at the top right-hand corner of Plate 49, fig. 1. Mineralog. Mus. Dresden. × *ca.* 20.

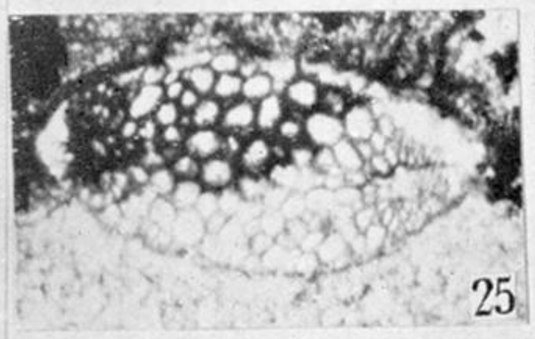
FIG. 10.—Chemnitz specimen, section from the lower end, showing details of stem stele and leaf-traces. The numerals 1–5 are placed opposite to the "pith"-rays. Two incipient leaf-traces are seen at 2 and 5, the latter with a central cavity presumably once occupied by a tissue similar to the "pith." The free leaf-trace on the left has only one protoxylem, that on the right has two; in both the adaxial xylem is less developed than the abaxial (*cf. Zalesskya* and *Thamnopteris*). Städt. Mus. Chemnitz. × *ca.* 14.

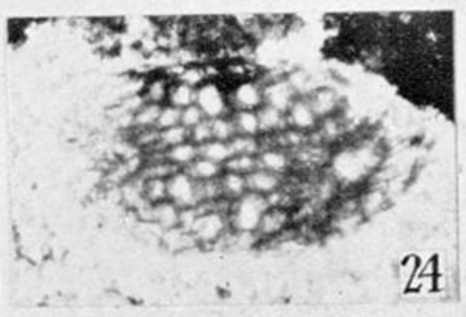


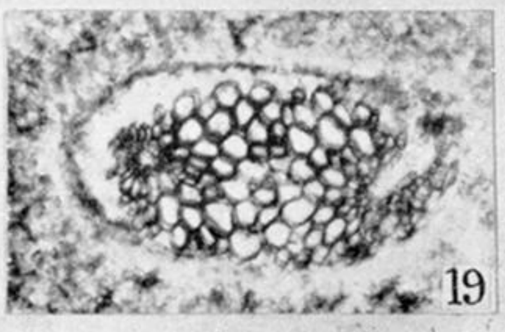


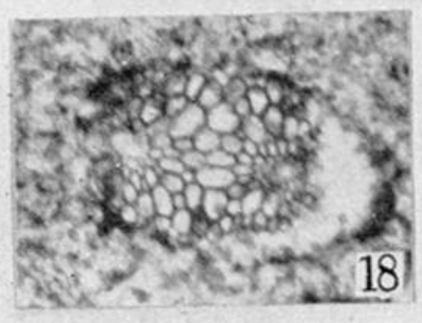


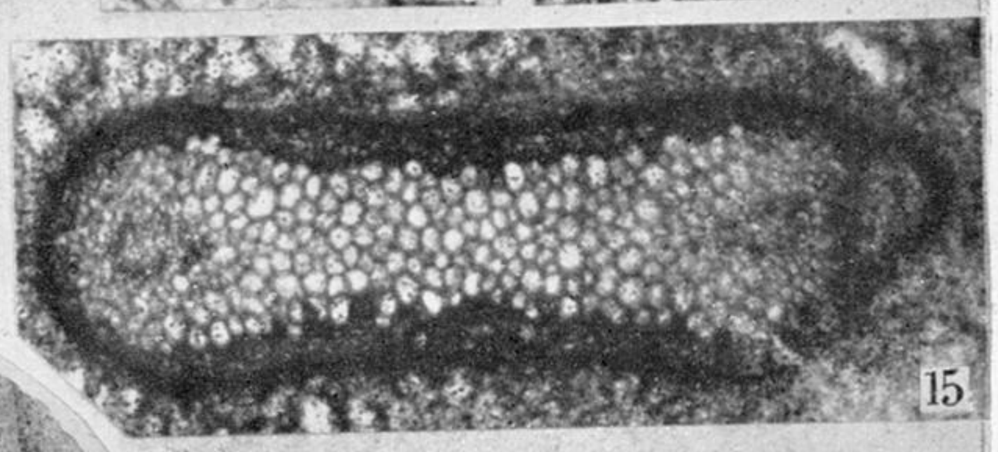


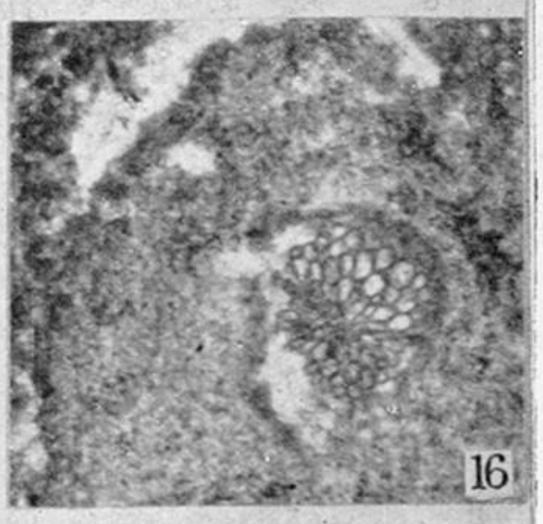


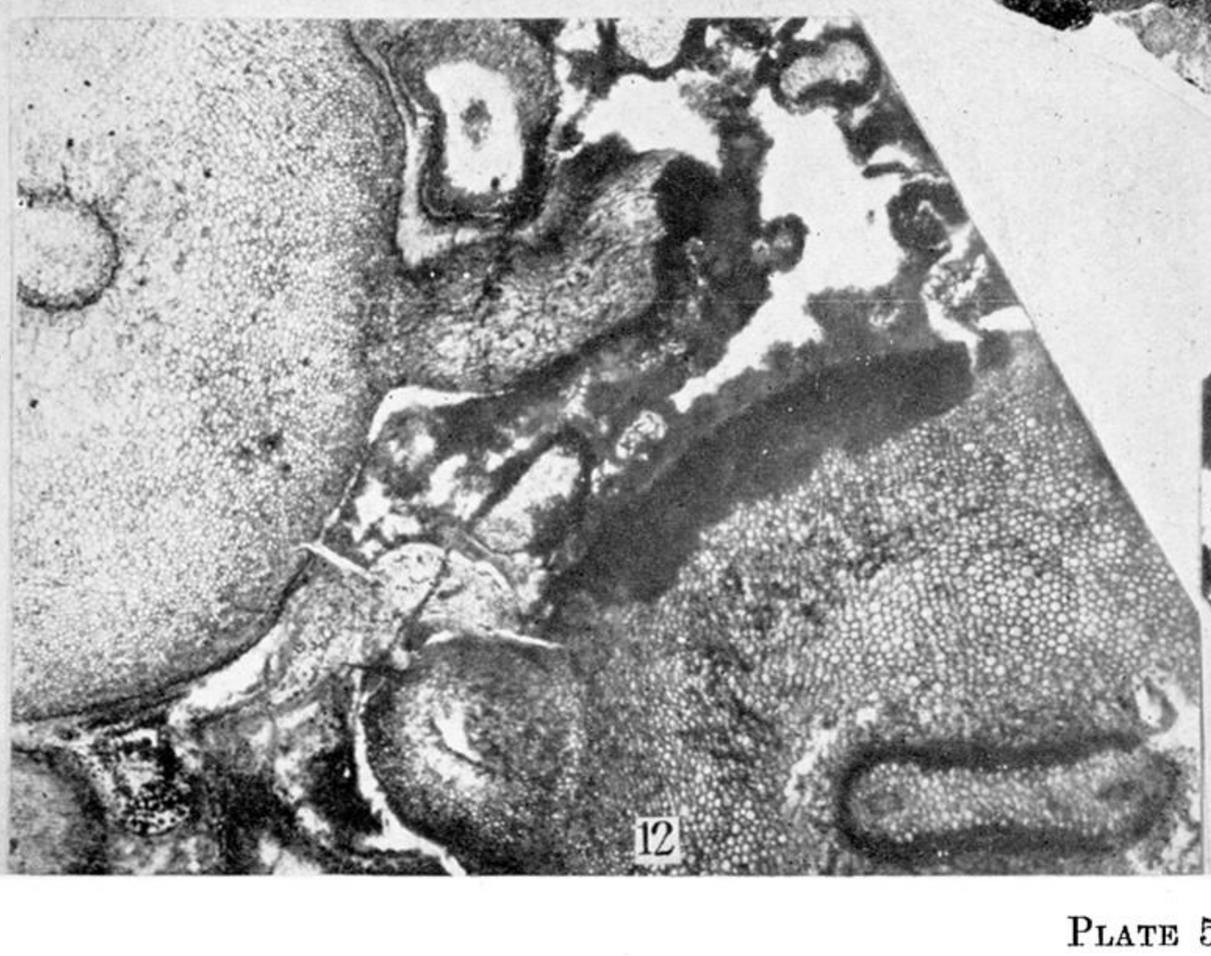












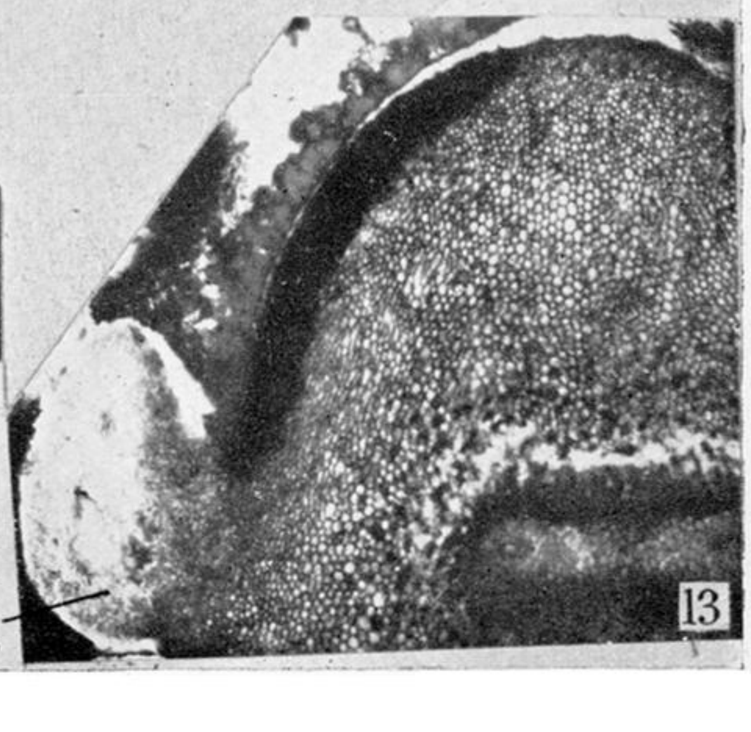


PLATE 51.

(All the figures are from untouched photographs.)

FIG. 11.—Chemnitz specimen, part of the same section (*cf.* Plate 49, fig. 3). Städt. Mus. Chemnitz. × 4.

FIG. 12.—LANGE'S specimen, section at 7 mm., showing the lateral appendages (? pinnæ or aphlebiæ) attached to two petioles. The appendage of the upper petiole is coming off at right angles to the leaf axis, that of the other seems to lie parallel to it. The latter petiole is seen cut 3 mm. higher up in fig. 15 ; and in that section there is no sign of this appendage, but the petiolar bundle is giving off a trace to an appendage on the opposite side. Mineralog. Mus. Dresden. × *ca.* 9.

FIG. 13.—LANGE'S specimen, section at 7 mm., the appendage seems to contain a pair of strands, but the preservation is too poor to show this for certain. Mineralog. Mus. Dresden. × *ca.* 9.

FIG. 14.—LANGE'S specimen, section at 13 mm., showing the structure of a root. × *ca.* 8·5.

FIG. 15.—LANGE'S specimen, section at 10 mm., showing the origin of a pinna- (or ? aphlebia-) trace from a point slightly abaxial to the actual margin of the petiolar trace. The same petiole is seen cut 3 mm. lower down in fig. 12. Mineralog. Mus. Dresden. × *ca.* 23.

FIG. 16.—LANGE'S specimen, section at 10 mm. A leaf-trace near its point of origin, already surrounded by its own cortex. The single protoxylem is nearer to the adaxial than to the abaxial margin (*cf.* fig. 10). Mineralog. Mus. Dresden. × *ca.* 25.

FIGS. 17–20.—LANGE'S specimen. Several bipolar leaf-traces from the same section (10 mm.). In fig. 19 one of the peripheral loops is damaged ; in fig. 17 one of the loops appears not yet to have been formed. In all the figures the adaxial side is turned downwards. All × *ca.* 25.

FIG. 21.—The same leaf-trace as in fig. 20. × *ca.* 65.

FIG. 22.—LANGE'S specimen, section at 7 mm. A well-preserved leaf-trace with the peripheral loops joined by a bridge of small tracheides (*cf.* Plate 50, fig. 8). Mineralog. Mus. Dresden. × *ca.* 25.

FIG. 23.—The same leaf-trace. × *ca.* 65.

FIGS. 24, 25.—LANGE'S specimen, section at 7 mm. Two fusiform leaf-traces (*cf.* Plate 2, fig. 8). Mineralog. Mus. Dresden. × *ca.* 25.