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X. *On the Structure and Affinities of* Dipteris, *with Notes on the Geological History of the Dipteridinæ.*

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(PLATES 47–49.)

THE name *Dipteris* was first used by REINWARDT* as a generic designation for a fern, which he named *Dipteris conjugata*, and defined as "Filix elegans, frondes duæ, in stipite communi elongato terminales, palmato-laciniatæ, dichotomo-nervosæ." BLUME,† in his 'Enumeratio Plantarum Javæ,' speaks of this species as *Polypodium Dipteris*, and KAULFUSS‡ adopts the same name. The 'Flora Javæ' by BLUME and FISCHER§ contains a good drawing of the rhizome and leaves of *Polypodium Dipteris*, the sporangia being represented as possessing the typical Polypodiaceous annulus. In the 'Icones Filicum' of HOOKER and GREVILLE‖ there is a coloured plate of an Indian fern described as *Polypodium Wallichii*, a name first used by ROBERT BROWN in the MS. list of species in the Wallich Herbarium (No. 287).¶ The same plant is referred to by WALLICH as *Polypodium macrocheiros*. In 1837, KUNZE** published a fairly satisfactory figure of a small frond of *Polypodium conjugatum*. It is in the 'Plantæ Javanicæ Rariores'†† that we find the most complete diagnosis of the species originally named by REINWARDT *Dipteris conjugata;* in this work ROBERT BROWN describes the Javan fern as *Polypodium* (*Dipteris*) *Horsfieldii*, using the term *Dipteris* as a sub-genus of *Polypodium*. He describes the characters of the sub-genus *Dipteris* as follows :—"Sori subrotundi, sparsi (v. transversim subseriati) inter (frondis palmatæ) venas primarias dichotomas earumque divisiones, venulis

* REINWARDT (28).

† BLUME (27).

‡ KAULFUSS (27).

§ BLUME and FISCHER (29), p. 174, Plate 81.

‖ HOOKER and GREVILLE (31), Plates 168 and 169.

¶ This collection is now in the possession of the Linnean Society of London.

** KUNZE (37), p. 16, Plate 10.

†† HORSFIELD and BENNETT (38), p. 1, Plate 1.

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divaricatissimis anastomosantibus insidentes. Indusium (verum) nullum. Caudex repens teres. Frondes elongato-stipitatæ binatæ; partiales dimidiatæ palmato-lobatæ. Venulæ secundariæ tertiariæ et ultimæ divaricatissimæ, crebre anastomosantes, penultimæ latere soriferæ, ultimæ apice vix dilatato libero. Indusium sporium vel (in *D. Horsfieldii*) pili sorum cingentes et capsulis intermixti; vel (in *D. Wallichii*) materia pulposo-gummosa capsulas immaturas obtegens."

The species named by BROWN *Polypodium* (*Dipteris*) *Horsfieldii* was discovered in 1814 by Dr. HORSFIELD, in Java, growing at a height of 5000 feet above sea-level. In describing this fern, BROWN draws attention to the existence of a "complete circle of *vasa scalariformia* separating the ligneous or fibrous vessels of the caudex into an inner and an outer portion," a feature, he adds, which "though not peculiar to *Dipteris*, seems to be of rare occurrence among ferns."

PRESL* refers to *P.* (*Dipteris*) *Horsfieldii* as *Phymatodes conjugata*, and FÉE,† in his 'Genera Filicum' adopts the name *Dipteris conjugata*, REIN., but incorrectly quotes *P. Wallichii*, HOOK. and GREV., as a synonym of REINWARDT'S species.

In 1853, HOOKER‡ described a new species of fern from Mount Ophir, near Malacca, under the name *Polypodium* (*Drynaria*) *Lobbianum;* he points out that the venation of this fern differs from that of *P. Horsfieldii* and *P. Wallichii*, and that the "binate character" of the frond of the two previously known species is not apparent in *P. Lobbianum*, in which the leaf has a digitate rather than a palmate form. Owing to the small size of the plate, the drawing given by HOOKER does not show the habit of the plant very clearly; there is no figure of the sporangia. MOORE§ mentions *Dipteris* as a genus including three species—*D. conjugata*, *D. Wallichii*, and *D. Lobbiana;* he includes the two former in the section *Eudipteris* and the latter in the section *Pseudodipteris*. In the 'Species Filicum'‖ and in the 'Synopsis Filicum,'¶ *Dipteris* is used as a sub-genus of *Polypodium;* in the latter work three species are described—*P.* (*D.*) *Dipteris* [= *P.* (*D.*) *Horsfieldii* in the 'Species Filicum'], *P.* (*D.*) *Wallichii*, and *P.* (*D.*) *Lobbianum*. In the second edition of the 'Synopsis Filicum,'** the name *P.* (*Dipteris*) *bifurcatum*, BAKER, is substituted for HOOKER'S name *P.* (*D.*) *Lobbianum*.

In 1888, BAKER†† instituted a new species of fern, discovered by the Bishop of Singapore and Sarawak in West Borneo, under the name *Polypodium* (*Dipteris*) *quinquefurcatum*. This type is described as allied to *P.* (*D.*) *bifurcatum* [= *P.* (*D.*) *Lobbianum*, HOOKER], but "the frond is four or five times dichotomously forked

* PRESL (36).

† FÉE (52), p. 274.

‡ HOOKER, W. J. (53), p. 309, Plate 11.

§ MOORE (57), p. 341.

‖ HOOKER, W. J. (64), vol. 5, p. 99.

¶ HOOKER and BAKER (68), p. 362.

** HOOKER and BAKER (83), p. 362.

†† BAKER (88), p. 260.

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with 18–20 lanceolate segments reaching 1 foot in length and above $\frac{1}{2}$ inch broad. Main veins evecto-patent, $\frac{1}{8}$–$\frac{1}{6}$ inch apart, prominently raised, connected much within the margin by a distinct cross-vein, each main areole thus formed containing usually 4-6 minute sori." No drawing accompanies the diagnosis;* a portion of the type-specimen is shown in fig. 18, Plate 48.

In Dr. CHRIST'S 'Die Farnkräuter der Erde'† the genus *Dipteris* is included in the Polypodieæ, a subdivision of the Polypodiaceæ, and in the recent account of ferns contributed by Dr. DIELS to the 'Natürliche Pflanzenfamilien' by ENGLER and PRANTL,‡ *Dipteris* is placed as the only genus in a special section, Aspidieæ-Dipteridinæ, and spoken of as an isolated type, the position of which cannot be definitely settled.

Before passing to the more detailed consideration of *Dipteris conjugata*, with which we are chiefly concerned, we may briefly draw attention to the chief distinguishing characteristics exhibited by the four known species of the genus.

DIPTERIS CONJUGATA, REINWARDT, Plates 47 and 49, and Plate 48, figs. 14–17, 19, 20, and 23.

[1823. *Polypodium palmatum*, WALLICH MS. (on sheet 286 in the Wallich Herbarium, Linnean Society's Library).]
[1823. *Polypodium Horsfieldii*, ROBERT BROWN MS. (Sheet 286, Wallich Herb.).]
1827. *Polypodium conjugatum*, KAULFUSS, p. 104.
1827. *P. Dipteris*, BLUME, p. 135.
1828. *Dipteris conjugata*, REINWARDT, p. 3.
1829. *Polypodium Dipteris*, BLUME and FISCHER, p. 174, Plate 81.
1836. *Phymatodes (Drynaria) conjugata*, PRESL, p. 198.
1837. *Polypodium conjugatum*, KUNZE, p. 16, Plate 10.
1838. *P. (Dipteris) Horsfieldii*, BROWN, HORSFIELD, and BENNETT, p. 1, Plate 1.
1852. *Dipteris conjugata*, FÉE, p. 274.
1857. *D. conjugata*, MOORE, p. 341.
1861. *Polypodium conjugatum*, METTENIUS, p. 78.
1864. *P. (Dipteris) Horsfieldii*, HOOKER, vol. 5, p. 99.
1865. *Dipteris conjugata*, SEEMAN, p. 369.
1865. *Drynaria Horsfieldii*, ETTINGSHAUSEN, p. 47.
1868. *Polypodium (Dipteris) Horsfieldii*, HOOKER and BENTHAM, p. 362.
1869. *Dipteris Horsfieldii*, BEDDOME, Plate 321.
1875. *D. conjugata*, SMITH, p. 196.

* Type-specimen (*Polypodium* 352*) in the Kew Herbarium.
† CHRIST (97), p. 122.
‡ DIELS in ENGLER and PRANTL (99), p. 202.

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1884. *Polypodium Dipteris*, BURCK, p. 88.
1886. *Dipteris Horsfieldii*, WALLACE, p. 31.
1897. *Polypodium* (*D.*) *Dipteris*, REINECKE, p. 357.
1897. *Dipteris conjugata*, CHRIST, p. 123, fig. 348.
1899. *D. conjugata*, DIELS, p. 202, fig. 108.

The lamina of the large frond is divided into two symmetrical halves by a deep median sinus; each half of the lamina is deeply lobed, and the edge of the broadly linear acuminate ultimate segments is serrate. The ultimate segments, which are rarely short and broad, terminating bluntly and traversed by several simple or forked veins (Plate 48, fig. 23), are usually long and narrow, frequently traversed by two veins, and occasionally by a single median vein. The main veins branch dichotomously and radiate through the lamina from the summit of the long and slender petiole in a palmate manner; they are connected by lateral veins, and these again are connected by tertiary veins, the delicate branches of which terminate freely within the more or less square or polygonal areolæ (Plate 47, fig. 10). The naked sori may be circular or oval (Plate 49, fig. 33) and often confluent; they vary much both in size and shape, and their individuality is often lost, as nearly the whole of the lower surface of the frond may be densely covered with a mass of sporangia. Filamentous paraphyses, terminating in a curved terminal glandular cell, accompany the sporangia (Plate 48, fig. 16). On a frond from which the sporangia have fallen their position is marked by patches of resinous secretion.

Localities.—Borneo, Malay Peninsula, Java, Luzon (Philippines), Samoa, Fiji, New Caledonia, Formosa, New Guinea, Yunnan (China; Dr. HENRY), New Hebrides, &c.

DIPTERIS WALLICHII (HOOKER and GREVILLE), Plate 48, figs. 11 and 22.

[1823. *Polypodium Wallichii*, ROBERT BROWN MS. (Type-specimen No. 287, Wallich Herbarium.) *P. Macrocheiros*, WALLICH MS. (Type-specimen No. 287, Wall. Herb.).]
1831. *Polypodium Wallichii*, HOOKER and GREVILLE, Plates 168 and 169.
1857. *Dipteris Wallichii*, MOORE, p. 341.
1864. *Polypodium* (*Dipteris*) *Wallichii*, HOOKER, vol. 5, p. 99.
1866. *Dipteris Wallichii*, BEDDOME, Plate 80.
1868. *Polypodium* (*D.*) *Wallichii*, HOOKER and BAKER, p. 362.
1875. *Dipteris Wallichii*, SMITH, p. 196.
1880. *Polypodium Wallichii*, CLARKE, p. 555.
1883. *Dipteris Wallichii*, BEDDOME, p. 334, fig. 184.
1897. *D. Wallichii*, CHRIST, p. 122.
1899. *D. Wallichii*, DIELS, p. 202.

This species resembles *D. conjugata* in habit, but the frond differs in the entire

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margin of the segments. The ultimate segments are usually linear in form and traversed by two veins; they may be bluntly terminated or prolonged into a linear acuminate tip, with a single median vein, not unlike the long and slender drip-tips of the leaf of *Ficus religiosa*, L. The sori are similar to those of *D. conjugata*, but they are somewhat less numerous, and the glandular paraphyses produce a greater amount of gummy secretion than in the preceding species.

Localities.—Sub-tropical region of Northern India, Assam, Cachar, Bhotan, Khasya (4000 feet), &c.

DIPTERIS LOBBIANA (HOOKER), Plate 48, figs. 12, 21, and 24.

1853. *Polypodium (Drynaria) Lobbianum*, HOOKER, p. 309, Plate 11.
1857. *Dipteris Lobbiana*, MOORE, p. 341.
1864. *Polypodium (Dipteris) Lobbianum*, HOOKER, vol. 5, p. 99.
1865. *Dipteris Lobbiana*, BEDDOME, Plate 233.
1868. *Polypodium (D.) Lobbianum*, HOOKER and BAKER, p. 362.
1875. *Dipteris Lobbiana*, SMITH, p. 196.
1876. *Polypodium (D.) bifurcatum*, BECCARI, p. 27, Plate 1, fig. 1.
1883. *P. (D.) bifurcatum*, HOOKER and BAKER, p. 362.
1883. *Dipteris Lobbiana*, BEDDOME, p. 336, fig. 186.
1884. *Polypodium (Dipteris) bifurcatum*, BURCK, p. 95.
1897. *Dipteris Lobbiana*, CHRIST, p. 123.
1899. *D. Lobbiana*, DIELS, p. 202, fig. 108.

The lamina of this species, which may reach a length of 30 centims., is readily distinguished by the narrow and linear form of the ultimate segments. The lamina is digitate rather than palmate, and the binate character is less obvious than in the two preceding species. The narrow segments, with entire margins, have a breadth of about 5 or 10 millims.; the midrib of each segment gives off lateral veins which form areolæ on either side (fig. 24, A, Plate 48). The sori agree with those of the other species; they often form a more or less regular single row on each side of the midrib.

Fig. 24, Plate 48, which is drawn natural size, represents the upper part of a frond referred by Dr. CHRIST, of Basel, to a variety of *D. Lobbiana*, which he names *D. Lobbiana*, var. *Ridleyi*. We are indebted to Dr. CHRIST's courtesy for the specimen shown in the figure, which was obtained from the Carimon Islands, near Singapore. This frond is similar to that of *Dipteris Lobbiana*, shown in fig. 21, but of smaller dimensions.*

Localities.—Mount Ophir, Malacca, Perak (5000–8000 feet), Borneo, Celebes, Java, Sarawak, Carimon Islands near Singapore.

* Dr. CHRIST has generously allowed us to give a drawing of this form of frond, a description of which has not yet been published.

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Dipteris quinquefurcata (Baker), Plate 48, figs. 13 and 18.

1888. *Polypodium* (*Dipteris*) *quinquefurcatum*, Baker, p. 260. [Type-specimen No. 352 in the Kew Herbarium.]
1897. *Dipteris quinquefurcata*, Christ, p. 122.
1899. *D. quinquefurcata*, Diels, p. 202.

The frond of this species is similar to that of *Dipteris Lobbiana;* the lamina is somewhat larger and the linear ultimate segments have a greater breadth (1·8 centims. in the type-specimen). The circular or oval sori with glandular paraphyses occur in the areolæ on either side of the midrib; the areolæ are larger than those in *D. Lobbiana* and contain more sori (Plate 48, fig. 18, A).

Locality.—Biululu, West Borneo.

The four species of *Dipteris* are characterised by the possession of a horizontal rhizome, which is densely covered with stiff brown scales of the type described in *D. conjugata,* and traversed by vascular tissue in the form of a tube (siphonostelic). The fronds of all species consist of a long and slender petiole and a large lamina, in some cases 50 centims. in length; in *D. conjugata* and *D. Wallichii* the lamina is divided by a deep median sinus into two symmetrical halves, but in *D. Lobbiana* and *D. quinquefurcata* the symmetrical bisection of the lamina is less obvious, the whole leaf being deeply dissected into narrow linear segments. The sori, which are without an indusium, consist of numerous sporangia and filamentous paraphyses terminating in glandular cells. The sporangia are characterised by the more or less oblique annulus and by the small output of bilateral spores. The sporangia of the same sorus are not developed simultaneously.

Dipteris conjugata.

The material on which the following account is based was obtained, in part, from Borneo by Mr. Robert Shelford, of Emmanuel College, Cambridge, Curator of the Sarawak Museum, and in part by Mr. Yapp, of Caius College, from the Malay Peninsula. The specimens from Borneo were gathered on Mount Santubong, at the mouth of the Sarawak River, at an altitude of 1500 feet, and the Malayan material was found on Gunong Inas (Perak), at an elevation of from 3700 feet to 4800 feet.*

(i.) *Rhizome.*—The dark-brown creeping stem (Plate 47, figs. 1 and 2) bears a very close resemblance in appearance and manner of growth to that of *Matonia pectinata,* R. Br. On the older rhizomes, which have a diameter of about 1 centim., there are usually but few leaves expanded at the same time; on the other hand, the more

* I wish to record my hearty thanks to my friends Mr. Shelford and Mr. Yapp for the trouble which they willingly took to obtain material in a condition suitable for microscopical examination.—(A. C. S.)

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slender stems bear several fully developed fronds. The whole surface of the stem is thickly covered with dark and stiff ramental "hairs," which lie parallel to the surface of the rhizome, and bend upwards at the base of each leaf, which they envelop in a dense brown felt (Plate 47, figs. 1 and 2). The ramenta are of sufficient interest to be considered in more detail. In the young condition, as they appear at the apex of a stem, the ramenta have the form of trichomes, consisting of cell-filaments (Plate 49, figs. 26, *r* and 36, *a*) terminating in a bluntly rounded apical cell; at a later stage they increase in length, the distal cells growing much longer and narrower (fig. 36, *b*), while the basal cells remain short and divide by radial longitudinal walls. In a tangential section through the apical portion of a rhizome, the young ramenta,—some of which consist of a single cell, while others appear as groups of four, twelve, or more cells,—present the appearance of oval or circular patches separated from one another by a dark irregular reticulum, which represents the surface of the rhizome seen between the young ramental outgrowths (Plate 49, fig. 34). Older ramenta, seen in a transverse section of the stem, appear as in fig. 9, Plate 47, and in fig. 8, *r*; the basal portion is multicellular and of irregular shape, the walls of the surface cells are dark brown and considerably thickened; the long and narrow portion of each ramentum lies along the stem surface, and being bent almost at right angles to the thick base, it is not shown in the transverse sections reproduced in figs. 8 and 9, Plate 47. Seen in side-view a ramentum appears as in figs. 29 and 30, Plate 49; the broad base attached to the surface of the rhizome has the outermost cells thickened and dark in colour; this is prolonged into a stiff, hair-like filament which may reach a length of 5 millims., and is composed of cells with dark brown walls, similar to those in the ramenta of various ferns described by GOEBELER.* The distal end of the bristle-like portion is often found to be composed of a few cells with thinner and colourless walls representing the remains of the apex of the ramentum, which remains actively growing and unthickened after the coloration has begun in the older cells. The alteration in the cell membranes extends in a basipetal direction from the median portion of a young ramentum, the apical cells retaining their power of growth for a considerable time. In the older ramenta the thinner internal cells of the basal portion may collapse and shrivel up, so that the outer cell-membranes, which are dark brown and thick, become detached in the form of a hollow cap. (Plate 49, fig. 29.) The long and strongly recurved ramenta of *Dipteris* bear a resemblance to those of *Botryopteris hirsuta* (WILL.) as figured by WILLIAMSON,† and they may be compared also with those of *Lyginodendron Oldhamium* (WILL.).‡

The apex of the rhizome terminates in a large single cell (Plate 49, fig. 26), which forms the summit of a conical elevation clothed in the basal region with filamentous ramenta. The longer and narrower cells shown in fig. 26, *d* mark the position of the

* GOEBELER (86), p. 477.

† WILLIAMSON (89), Plate 4, figs. 9 and 10.

‡ WILLIAMSON (90), Plate 12, fig. 8.

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desmogen strands, which pass gradually into the tubular stele of the rhizome. The stelar-tissue terminates in the apical region of the stem as a flat or slightly depressed rounded arc, which is interrupted immediately behind the apex, where the origin of the youngest leaf causes a break or gap slightly to one side of the termination of the stele. The photograph reproduced in fig. 8, Plate 47, illustrates the appearance of the mature stele, which has the form of a tube, limited both externally and internally by an endodermis (Plate 47, fig. 7, *e.*); the xylem is enclosed on both faces by a band of phloem (fig. 7, *ph.*). As we follow the stelar tissue from the apex of the stem, the first lignified elements to make their appearance are the narrow spirally thickened tracheids, which appear as distinct groups of protoxylem occupying a central position in the ring of unlignified and larger tracheids (Plate 47, figs. 4 and 6, *px.*; Plate 49, fig. 32, *px.*). Each group of protoxylem elements is associated with a few xylem parenchymatous cells (fig. 7, Plate 47). The structure of an older portion of the stem is shown in figs. 7 and 8, Plate 47; the extra-stelar tissue consists of a broad band of dark-brown cells, from the surface of which project the irregular ramental outgrowths. This peripheral thick-walled tissue is succeeded by a broader band of ground-tissue composed of larger and thinner walled cells bearing numerous simple pits; nearer the stele the parenchymatous cells become smaller and their walls increase in thickness. Internal to the tubular stele the ground-tissue consists of ordinary parenchyma similar to that of the extra-stelar region. The endodermis is clearly marked off from the rest of the ground-tissue by its more closely fitting cells, of which the distinct but delicate radial walls are often torn in the process of section-cutting, or they may appear as more or less folded membranes (fig. 7, *e.*). The pericycle (Plate 47, fig. 7, *pc.*), consisting of two or three rows of cells, is succeeded by the phloem, composed of sieve-tubes and parenchymatous elements; the limits of the phloem on both the inside and outside of the stele are clearly defined by the occurrence of a band of smaller and thicker walled elements which constitute the protophloem (Plate 47, fig. 7, *pt.*; Plate 49, fig. 32, *pt.*), and consist in the main of sieve-tubes characterised by fairly stout walls and numerous lateral sieve-plates (Plate 49, fig. 28, and fig. 32, *sv.*). The xylem has the form of a hollow cylinder four to five elements in breadth, and consists of scalariform tracheids, median groups of spiral protoxylem elements, and a few parenchymatous cells. An occasional large and thin-walled cell containing tannin is met with in the middle of the xylem tissue (Plate 49, fig. 32, *t.*). Internal groups of ordinary xylem-parenchyma occur here and there associated with the tracheids, and occasionally a narrow band of these elements stretches across the xylem and breaks the continuity of the tracheal zone. The rhizome of *Dipteris conjugata* is frequently branched in a dichotomous manner; shortly before the forking occurs, the stele becomes transversely elongated in the form of an ellipse (fig. 37, *a*, Plate 49), a median constriction is then formed (fig. 37, *b*), and finally the single stele splits into two, one of which, as shown in fig. 37, *a* and *b*, is slightly bulged outwards to give off a branch to a young leaf.

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(ii.) *Root.*—The strong wiry roots are given off from any part of the surface of the stem (Plate 47, figs. 1 and 2); two of these are shown in figs. 7 and 8, *Rh.*, penetrating the extra-stelar tissue. Each root arises from a group of narrow tracheids situated on the outer edge of the xylem (fig. 7, *Rh.*); this rhizogenous xylem contains several short and somewhat twisted tracheids. The triarch stele of the root is succeeded by a well-defined endodermis, which is enclosed by three or four layers of dark-brown elements with very thick walls.

(iii.) *Leaf* (Plate 48, figs. 17, 19, 20 and 23).—The form of a typical frond of this species is shown very clearly in the large plate in the 'Plantæ Javanicæ Rariores.'* The long and slender petiole, which may reach a length of more than 1 metre, forks at the summit into two equal portions, which bend apart and form a fork which may be compared with the gap between two fingers of the hand stretched apart; seen from the upper face the base of the fork is represented by an almost straight line or edge as in the human hand, while from the under surface the base of the fork is prolonged downwards into a gradually narrowing groove precisely similar to that between the fingers of a hand seen in back-view (Plate 48, fig. 17). From each half of the petiole stout branches are given off which radiate in a palmate manner through the lamina. The forking of the petiole produces the characteristic bisected form of the leaf. The inner edge of each half of the frond forms an upward continuation of two branches of the petiole, but the edges of the two portions gradually bend inwards until the halves of the lamina overlap (Plate 48, figs. 17 and 20). The edges of the median sinus may be described as following an ogee curve, bending outwards from the summit of the leaf-stalk, and then gradually curving inwards. Each of the main ribs is repeatedly branched dichotomously on its way through the lamina; the narrower ultimate segments have a single midrib, on each side of which the lateral veins form areolæ like those in the linear segments of *Dipteris Lobbiana* and *D. quinquefurcata.* Cross veins arise at right angles to the main veins, and form more or less straight connecting ribs; from these again smaller veins are given off at right angles, forming rectangular or polygonal meshes, from the sides of which finer veins arise and end freely in the leaf mesophyll (Plate 47, fig. 10). The sori, which are situated above the finer veins, are accompanied by numerous filamentous paraphyses (Plate 49, fig. 33, *p.*), terminating in a curved swollen cell, which serves as a secretory gland (Plate 48, fig. 16). The young leaves bear numerous filamentous hairs, which in dried specimens appear as a rich brown felt, and persist in comparatively large fronds on the still elongating apical regions of the narrow segments, extending some distance along the main ribs (Plate 47, fig. 10).

The petiole of a leaf reaches a considerable length before the lamina begins to unfold (Plate 47, fig. 2). The younger leaf shown in fig. 20, Plate 48, has a length of 39 centims., but the lamina is hardly visible. A young frond in the British Museum Herbarium, collected by Dr. FORBES in South-east Java, has a leaf with a petiole

* HORSFIELD and BENNETT (38), Plate 1.

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nearly 70 centims. long, terminating in a partially expanded lamina 3 centims. long and 2 centims. broad; the lamina and upper part of the petiole are clothed with woolly hairs. It is important, from the point of view of the determination of fossil leaves, to notice the variation in the form of the frond in *Dipteris conjugata*. Slender rhizomes bear leaves which differ considerably in appearance from those on older stems; the smaller type of frond is characterised by fewer and wider lobes, and is relatively much broader than the larger and more typical fronds. A common form of small frond is represented in fig. 19, Plate 48; this leaf, which is without hairs, and apparently mature, is 10 centims. broad. The expanded leaf shown in fig. 20, Plate 48, illustrates a type intermediate between that represented in fig. 19 and a frond of full size. A small leaf of a plant in the Kew Herbarium, from Mount Dayman, New Guinea (Plate 48, fig. 23), is remarkable for its almost orbicular form, the absence of the deep median sinus, and for the bluntly rounded, short and broad lobes in place of the usual long acuminate segments. The lamina shown in the figure (Plate 48, fig. 23) is 14 centims. deep and 19·5 centims. broad. Other forms of leaves have been figured by KUNZE and DIELS.*

A portion of the lamina of a young leaf is shown in transverse section in fig. 27, Plate 49. Between the upper and lower epidermal layers, composed of large cells, are enclosed two bands of narrower cells with regular radial walls, interrupted at intervals by the occurrence of groups of smaller elements formed by tangential divisions in the larger cells. The groups of small cells (*v.*) mark the position of the leaf-veins. Long filamentous hairs, containing a secretion in their somewhat capitate apical cells, occur abundantly on the lamina of a young leaf, being particularly abundant on the prominent projecting ribs below the main veins. The incurved apex of a young leaf-bud with its partially differentiated meristele, presents a very close agreement with that of *Matonia pectinata*.†

The stomata, which are confined to the lower surface of the lamina and slightly sunk, consist of a pair of guard-cells partially overarched by two epidermal cells, which form a kind of vestibule in front of the stomatal pore. The outer walls of the lower epidermal cells are often slightly arched outwards in the form of blunt papillæ. The mesophyll presents no features of special interest; it consists of more or less stellate cells, and in the lower half of the lamina the structure is very lax. Some of the veins are collateral in structure; each xylem and phloem strand is enclosed by a well-defined sheath of large tangentially elongated cells with slightly lignified walls. Towards the termination of a vein the xylem elements become broader, and form a group of storage-tracheids similar to those in certain xerophytic flowering plants. Each vein is accompanied by a strand of mechanical tissue, and similar thick-walled cells occur at the free edge of the leaf lamina where they no doubt serve as a protection against tearing.‡

* DIELS (99), p. 202.

† SEWARD (99), Plate 19, fig. 30.

‡ HABERLANDT (96), p. 169.

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The structure of a petiole is illustrated by fig. 3, Plate 47. An epidermis of small cells is succeeded by a hypodermal band of thick-walled cells, which pass gradually into larger and thinner elements nearer the meristele. The stele is broadly U-shaped, the upper end of each arm being curved inwards in the form of a spiral. The endodermis is succeeded by a pericycle, usually two cells wide, composed of thin-walled cells of unequal size. On the outer edge of the stele the protophloem (Plate 49, fig. 25, *pt.*) forms a continuous and well-defined band of small and comparatively thick-walled elements. The protophloem (fig. 25, *pt.*) is confined to the phloem zone on the outer edge of the xylem; on the inside of the xylem the sieve-tubes and parenchyma form a broader band than that on the outer face of the xylem. The elements of the xylem form a narrow band, often reduced to one tracheid in width, and occasionally interrupted by xylem-parenchyma; numerous groups of protoxylem occur on the inner edge of the xylem (fig. 25, *px.*). The meristele is thus endarch, while the xylem of the rhizome stele is mesarch in structure. The protoxylem strands, of which there may be as many as fifty, are very clearly shown in sections of young leaf-stalks stained with gentian violet and eosin. Next the protoxylem strands the tissue is often more or less torn, forming a fairly regular canal or an irregular gap. A striking characteristic of the internal phloem is the occurrence of groups of tannin sacs between each protoxylem group (Plate 49, fig. 25, *t.*). A few secretory cells occur also in the external phloem. The groups of secretory sacs, which form a conspicuous feature in the petiole stele (Plate 47, fig. 3, *t.*), are formed at an early stage in the development of the leaf; in fact, they appear to be among the earliest differentiated elements. The secretory elements are clearly shown in the section of a fairly young petiole, reproduced in Plate 47, fig. 5, *t.*

The diagrammatic sections shown in Text-figure 1 illustrate the behaviour of the petiole stele as it alters its form a short distance below the summit of the petiole, and

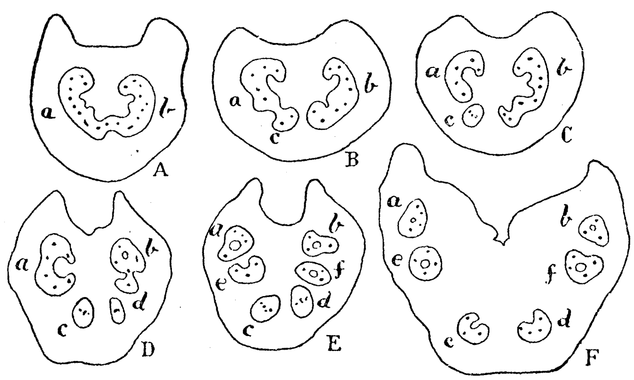

Fig. 1.

gives off branches to form the main ribs of the lamina. The black dots in the vascular tissue indicate the position and number of the protoxylem strands. A short distance

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below the fork of the leaf-stalk the stele becomes constricted into two slightly unequal portions (Plate 47, fig. 5; text-fig. 1, A, *a* and *b*); from the lower end of one of them a small vascular strand, *c*, is given off. At a higher level in the petiole a similar strand is detached from the smaller portion of the stele (section C and D *d*). In the section shown in text-fig. 1, D, the alternate branching has reached a further stage; the curved meristele, *a* (text-fig. 1, D), is gradually enclosing a piece of ground-tissue, while the stele *b* consists in the upper part of a concentric stele with an axial group of ground-tissue and an internal and external endodermis; from the lower portion a small strand is almost detached. At a somewat later stage (section E) we find the strands *a* and *b* replaced by four separate strands; of these *a*, *b*, and *f* are tubular, the vascular tissue being enclosed both internally and externally by a well-defined endodermis (Plate 49, fig. 31, *e* and *e'*). In section F the two lower strands *c* and *d* are closing on themselves to assume the tubular form of *a*, *e*, *b*, and *f*. In sections cut through the lamina at a slightly higher level than that represented by F (text-fig. 1), the depression on the upper face of the petiole is much deeper, and owing to the growth of the mesophyll between the main veins, the individual vascular strands are further apart. Fig. 38, Plate 49, represents a vascular strand traversing one of the main ribs of a leaf; its form is similar to that of the small strands *c* and *d*, diagrammatically shown in text-fig. 1, D–F; there are three groups of protoxylem, a large one in the middle of the concave side, and one terminating each arm of the crescent (fig. 38, *px.*); the protophloem (*pt.*) is clearly shown as an arc on the convex side of the xylem. Two large groups of secretory sacs (*t*, *t*) occur in the phloem, which is partially enclosed by the xylem, and a strand of thick-walled elements (*f*) is seen in the patch of parenchyma midway between the two arms of the xylem-arc. A precisely similar occurrence of thick-walled cells is described by POIRAULT in the petiolar stele of *Gleichenia speluncæ*.* In Plate 49, fig. 31, one of the tubular steles of a leaf (*b*, text-fig. 1, F) is shown on a larger scale. The internal and external endodermal layers (*e* and *e'*) are readily identified by the dark radial walls; as the petiole from which the section was taken was young, the protoxylem tracheids are the only lignified elements (*px.*); large secretory sacs (*t*, *t*) occur in the inner phloem, while those shown at *t'* interrupt the continuity of the xylem-ring. The axial region is occupied by parenchymatous ground-tissue. This form of stele is very similar to that characteristic of the stem of *Marsilia*.

Origin of Leaf-trace.—In a transverse section of a rhizome immediately behind a leaf (Plate 47, fig. 6), the stele is seen to have become longer in a vertical direction, the dorsal portion having the form of a semicircular arc; this arc gradually detaches itself from the siphonostele and bends upwards into the leaf. The segment of the rhizome stele which passes into the leaf has tracheids of somewhat narrower diameter than those in the stem, and the xylem of the U-shaped meristele is

* POIRAULT (94), p. 181, fig. 17.

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narrower than that of the main stele, and has an endarch instead of a mesarch structure. The narrower form of the petiole is clearly shown in the sections reproduced in figs. 4 and 6, Plate 47. The section reproduced in fig. 4, Plate 47, shows also that in the region where the gap in the stele is about to be formed by the separation of the leaf-stele, the vascular tissue has become wider (fig. 4, *b*, *b*), so that the future leaf-stele rests on broad bases; these broader portions of the stele are gradually invaded by ground-tissue (figs. 4 and 6, *g*, Plate 47), which forms a narrow bay in the lower part of the meristele, and this eventually gives rise to the incurved free edge of the leaf-stele, which forms a marked feature in the vascular tissue of a mature petiole. The section reproduced in fig. 4, Plate 47, shows the foliar gap on one side of the rhizome stele, while on the other side the lower margin of the leaf-stele is still in continuity with the broad portion of the vascular cylinder of the stem. The gap formed in the rhizome stele by the splitting off of the meristele becomes closed a short distance in front of the leaf; the position of the foliar gap in relation to the leaf is diagrammatically shown in fig. 35, Plate 49, which represents a longitudinal vertical section of a rhizome passing through the base of a leaf.

Systematic Position of Dipteris.

It has been customary to include *Dipteris* in the Polypodiaceæ, and several authors have referred this Indo-Malay type to the genus *Polypodium*. The removal of *Dipteris* by Dr. Diels* to a special section of the Polypodiaceæ, which he names Aspidieæ-dipteridinæ, expresses his view that the genus must be looked upon as an isolated type. Some years ago Professor Zeiller† drew attention to the resemblance between the fronds of *Dipteris* and certain fossil ferns of Mesozoic age, and more recently‡ the same author has demonstrated afresh the striking similarity between the extinct and recent forms. It was primarily Professor Zeiller's reference to *Dipteris* as probably an ancient type that led to the present investigation.

In a note communicated to the British Association§ in September 1900, we expressed the view that *Dipteris* should be removed from the Polypodiaceæ and placed in a family apart; one of us|| has since given definite expression to this opinion by adopting the family name Dipteridinæ to include the recent species, as well as such fossil genera as *Dictyophyllum* and *Protorhipis*. It has been generally assumed that the sporangia of *Dipteris* agree with those of typical Polypodiaceæ in having a vertical annulus, and such few drawings as have been published bear out this view.

* Diels (99).

† Zeiller (82), p. 313.

‡ *Ibid.* (97), p. 51.

§ Seward and Dale, 'Report Brit. Assoc. (Bradford),' 1900, p. 946.

|| Seward (00), p. 17, and (00^2), p. 17.

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An examination of the sporangia of *Dipteris* shows that the four species of the genus agree in the oblique position of the annulus and in the absence of a clearly defined stomium (Plate 48, figs. 11–16). The sporangia of the different species are fairly uniform in size, being about ·02 millim. in length; the short stalk consists of four rows of cells, and the spores are few and bilateral. The annulus varies to some extent in position; in some cases it may appear to be vertical (*e.g.*, fig. 14, Plate 48), but a closer inspection from different points of view usually demonstrates that the annulus cells do not follow a strictly vertical course. In the sporangium shown in fig. 15, Plate 48 (*Dipteris conjugata*), the annulus is obviously oblique, and suggests a Cyatheaceous fern; in fig. 11 the annulus is seen to be strongly convex, while the wall of the sporangium is comparatively flat; seen from the other side the annulus cells would appear much smaller (*e.g.*, fig. 14), and the sporangial wall would be found to be curved. The curvature of the sporangium is clearly shown in figs. 12 and 13; this bent form of the sporangium and the obliquity of the annulus are features characteristic of the genus. In the sporangium represented in fig. 12 (*D. Lobbiana*) the annulus is seen to bend over the apex of the sporangium; similarly in fig. 13 (*D. quinquefurcata*) the annulus cells are shown passing up one side of the sporangium, then bending over the top, and passing down in a different plane over the convex surface of the curved sporangium. This twisted form of annulus reminds one to some extent of *Matonia*, but the agreement between the sori of these two genera is by no means a close one.* In *Dipteris* the sori are without an indusium, the sporangia are not developed simultaneously, but different stages are represented in one sorus (division "Mixtæ" of BOWER), and the number of sporangia is much greater. Some sporangia of *Alsophila excelsa* figured by BOWER† in his recent memoir on the Leptosporangiate ferns, bear a close resemblance to those of *Dipteris* in the oblique annulus and in the structure of the stalk. The genus *Thyrsopteris*‡ may also be compared with *Dipteris* in the obliquity of the annulus and in the curved form of the sporangium. The oblique annulus of *Plagiogyria* (a name used by METTENIUS§ and some other authors as of generic rank, but by others as a section of the genus *Lomaria*) suggests another comparison with *Dipteris*, but the annulus of the latter genus is further characterised by being slightly twisted as well as oblique, and in other respects the resemblance between these two types is not very close.‖

The most striking anatomical character of *Dipteris*, as represented by the four species, is the tubular form of the stele. VAN TIEGHEM'S term "solenostely" has

* BOWER (99), Plate 4, figs. 58–62; SEWARD (99), Plate 18, figs. 18–20.

† BOWER (99), Plate 5, figs. 88, 89.

‡ BOWER (*loc. cit.*), Plate 6, figs. 106–115.

§ METTENIUS (56).

‖ After noticing the obliquity of the annulus in the sporangia of *Dipteris*, one of us wrote to Professor BOWER and found that he recognised the genus as having sporangial characters which do not conform to those of true Polypodiaceæ. Professor BOWER'S more detailed researches into the structure and development of the sori of *Dipteris* may place us in a position to discuss more fully the affinities of the genus.

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recently been revived by GYWNNE-VAUGHAN* as a convenient one to apply to stems "in which the vascular tissue is arranged in a simple hollow cylinder with phloem and phlœoterma on either side, the complete continuity of which is interrupted only by the departure of the leaf-traces; the gaps thus produced being closed up in the internode above the departure of the next leaf-trace."* Dr. JEFFREY,† of Toronto, has suggested another term, "siphonostelic," to include tubular steles, but he uses this designation in a more comprehensive sense; the stele of *Dipteris* would be spoken of in JEFFREY'S terminology as being of the amphiphloic siphonostelic type. In considering the affinities of *Matonia pectinata*, one of us referred to several other ferns in which the stem possesses a tubular stele; the conclusion arrived at was that "the annular form of stele is not of great systematic importance."‡ On the other hand, Mr. GWYNNE-VAUGHAN regards "the solenostely of the stem and the peculiar horse-shoe shape of the petiolar meristele as characters of primary importance, and of considerable reliability."§ This investigator has definitely taken in hand a series of observations on the anatomy of solenostelic ferns, which will no doubt furnish us with the necessary data towards forming an estimate of the value of the solenostelic structure, both as a criterion of affinity and as evidence in phylogenetic considerations.

The stele of *Dipteris*, as represented by the four living species, agrees with that of *Loxsoma* in its tubular form, and in the manner of origin of the leaf-traces. The agreement between *Loxsoma* and *Dipteris*, as regards the origin of the leaf-traces, does not extend to the minute anatomy; in the former genus the spiral protoxylem elements of the meristele are not connected with the scalariform protoxylem of the rhizome stele,‖ whereas in *Dipteris* the spiral tracheids of the stele and meristele are in continuity. A similar resemblance exists between *Dipteris* and such ferns as *Pteris incisa*, *Hypolepis tenuifolia*, *Davallia strigosa*, *D. Speluncæ*, and *Dennstædtia davallioides*. The more complex types, such as *Matonia pectinata*, *Thyrsopteris elegans* and *Dennstædtia rubiginosa*, differ from *Dipteris* in the occurrence of two instead of one tubular stele (*Matonia*), or in having one or more vascular strands internal to the single solenostele (*Thyrsopteris* and *Dennstædtia rubiginosa*). The various species of solenostelic ferns differ from one another more or less widely as regards anatomical details. The stele of *Dipteris* presents a fairly close agreement with those of *Dennstædtia davallioides* and *Hypolepis tenuifolia* as regards general structure and in the mesarch position of the spiral protoxylem tracheids; in the two latter features *Dipteris* differs from *Loxsoma*, in which the xylem is exarch and the protoxylem elements are scalariform and not spiral. The horse-shoe form of the leaf-

* GWYNNE-VAUGHAN (01), p. 73.

† JEFFREY (99) and (99[2]).

‡ SEWARD (99), p. 190.

§ GWYNNE-VAUGHAN (01), p. 90.

‖ *Ibid.*, p. 86.

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trace of *Dipteris* is a feature common to many ferns; in the presence of secretory cells *Dipteris* agrees with certain members of the Cyatheaceæ and with the Osmundaceæ.* The triarch structure of the roots is a character which *Dipteris* shares with *Matonia*, as well as with some species of Cyatheaceæ, Gleicheniaceæ, Hymenophyllaceæ, and Ophioglossaceæ.

In view of the work now in progress by Mr. GWYNNE-VAUGHAN, Dr. JEFFREY, Mr. BOODLE, and others, it is premature to discuss at greater length the affinities of *Dipteris* as indicated by anatomical characters. We are of opinion that the anatomical features, taken in conjunction with the sporangial characters and the characteristic form and venation of the fronds, afford ample reasons for the removal of the genus *Dipteris* from the Polypodiaceæ, and its inclusion in a separate family, of which it represents the solitary surviving type.

GEOLOGICAL HISTORY.

The genus *Dipteris* represents a type which has descended from the Mesozoic period with but little modification; this at least is the conclusion to which we are led by the examination of a considerable amount of evidence furnished by fossil fronds. The records of the past history of the Dipteridinæ consist of leaves—often preserved in unusual perfection—on some of which sori and sporangia have been found in sufficiently good condition to enable us to recognise the structure of the sporangia. The paucity of petrified fragments of plants in Mesozoic strata is a serious obstacle in the way of a satisfactory reconstruction of extinct types, but in the case of *Dipteris* the external characters are of a distinctive kind, and of more systematic value in this genus than they are in the great majority of ferns. This is not the place to enter into a detailed discussion of the synonomy of the possible fossil representatives of the Dipteridinæ; we are more directly concerned with the value of the evidence which can be adduced in support of the statement that the Indian and Malayan species of *Dipteris* are remnants of a family with a wide European distribution during the earlier part of the Mesozoic epoch.

One of us† has recently discussed the relationship of several Jurassic genera described under the names *Dictyophyllum*, *Clathropteris*, *Thaumatopteris*, *Camptopteris*, *Hausmannia*, and *Protorhipis*; and reasons have been given for abandoning *Hausmannia* and *Thaumatopteris* and retaining the other generic designations for extinct members of the Dipteridinæ.

Dictyophyllum.—This genus, founded by LINDLEY and HUTTON in 1834,‡ is characterised by the large size of the palmate fronds, which are deeply dissected into broadly linear pinnatifid lobes; each lobe is traversed by a stout midrib giving

* SEWARD (99), p. 190; PARMENTIER (99), p. 303.

† SEWARD (00), p. 119.

‡ LINDLEY and HUTTON (34).

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off lateral veins, one to each ultimate segment; tertiary veins, which are given off approximately at right angles, form polygonal or rectangular meshes occupied by the ultimate ramifications of the vascular bundles. The sori, which are more or less circular in form, occur abundantly on the under surface of the lamina, and consist of several sporangia with a well-defined annulus. It is not possible to speak with certainty as to the exact position of the annulus. The spores appear to be tetrahedral. With the exception of a few fossil stems described by NATHORST from the Rhætic plant-beds of Scania as *Rhizomopteris* (*Dictyophylli*) *major*, NATH., and *R. Schenki*, NATH.,* and by ZEILLER† from the Rhætic strata of Tong-King, the Mesozoic ferns referred to the Dipteridinæ are represented solely by fronds. It is probable, as NATHORST suggests, that *Rhizomopteris* bore *Dictophyllum* leaves; the rhizomes are characterised by dichotomous branching, and by the occurrence of horse-shoe shaped scars of leaf-traces. Fronds identical with those referred to *Dictyophyllum* have been placed in BRONGNIART'S genus *Clathropteris*, but as the main difference consists in the more rectangular form of the meshes formed by the anastomosing veins, the latter name need hardly be retained. Similarly, the leaves formerly placed in the genus *Thaumatopteris* should be transferred to *Dictyophyllum*. Another generic name—*Camptopteris*—is sometimes applied to fronds which cannot reasonably be separated from *Dictyophyllum*, but it may be a convenience to retain this designation for certain ferns described by NATHORST from the Rhætic Coal-Measures of Scania, and represented by the species *Camptopteris spiralis*, NATH. A restoration of this fern, published by NATHORST in his 'Geology of Sweden,'‡ admirably illustrates the habit of the genus; the frond has a long petiole, which bifurcates at the top into slightly divergent arms bearing numerous linear pinnæ; the pinnæ are disposed spirally on the branched rachis; both the venation and the soral characters appear to agree with those of *Dictyophyllum*. In all probability this striking fern may be safely included in the Dipteridinæ.

Protorhipis.—This genus was instituted by ANDRAE in 1853§ for a Jurassic plant from Steierdorf, which he named *Protorhipis Buchii*. The type-specimen is thus described by ANDRAE:—"Fronde late sinuato-dentata, venis primariis pluries dichotomis validis remotis, venis secundariis et venulis tenerrimis." The fronds referred to this genus are smaller than those included in *Dictyophyllum*; the lamina may be more or less orbicular in shape, with a serrate or irregularly lobed margin, and traversed by several palmately disposed main veins, from which anastomosing branches are given off as in *Dictyophyllum* and *Dipteris*, or it may be deeply dissected into linear segments. The latter form is represented by such fossil fronds as

* NATHORST (78), p. 10, Plate 1, figs. 8–13; (86), p. 40, Plate 1, fig. 1.

† ZEILLER (82), p. 312.

‡ NATHORST (92), p. 169.

§ ANDRAE (53), p. 36. A figure of ANDRAE'S type-specimen is given also by WARD (96), Plate 106 fig. 1.

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those from a Jurassic horizon in Bornholm described by BARTHOLIN as *Hausmannia Forchhammeri*,* but which ZEILLER† has shown cannot be separated generically from *Protorhipis*. Attention has already been drawn to the probable identity of the Wealden fossils included by DUNKER and SCHENK in *Hausmannia*, with those described as *Protorhipis* or *Dictyophyllum Roemeri*.‡ The most interesting specimens of *Protorhipis* from the point of view of a comparison with *Dipteris*, are those recently figured by ZEILLER§ from the same locality from which ANDRAE described his type-specimen; they show in a particularly striking manner the close correspondence between the fossil fronds and those of *Dipteris conjugata* and *D. Wallichii*.

In the case of some specimens it is practically impossible to decide between *Protorhipis* and *Dictyophyllum* as the most suitable name; it is not improbable, as SAPORTA‖ suggested, that the apparent generic distinction may be merely an expression of the difference in size and form between leaves of the same plant. The lower portion of a *Dictyophyllum* frond might well be referred to *Protorhipis* (*e.g.*, a specimen figured by SCHENK from Rhætic beds in China¶), and it must be admitted that, while we retain both names, it is possible that a true generic distinction does not exist. It was suggested by SAPORTA** and LESTER WARD†† that some at least of the fossils referred to ANDRAE'S genus *Protorhipis* should be considered as angiosperms rather than ferns. SAPORTA described some oval or suborbicular leaves from the lower Cretaceous rocks of Portugal under the name *Protorhipis Choffati* which he placed in his class "Proangiosperms," and the same species is included by WARD, with some other examples of *Protorhipis*, among "Archetypal Angiosperms." SAPORTA'S Portugal plant, as ZEILLER has pointed out, does not possess the venation characters typical of *Protorhipis;* the main veins are more numerous and less regular, and the meshes formed by the finer veins are less uniform in size and shape. In all probability *Protorhipis Choffati*‡‡ is a fern agreeing more closely with the smaller "bracket-leaves" of *Platycerium* than with the frond of *Dipteris*. It is at least clear that the true *Protorhipis*, which is an undoubted fern very similar to *Dipteris*, does not throw any light on the possible origin of Angiosperms.

The following list is intended to illustrate in a concise form the distribution in space and time of such fossil ferns as we believe may be reasonably regarded as members of the Dipteridinæ. Species founded on doubtful or too fragmentary

* BARTHOLIN (94), p. 26, Plates 11 and 12.

† ZEILLER (97), p. 51.

‡ SEWARD (94), p. 140.

§ ZEILLER (97), Plate 21.

‖ SAPORTA (73), p. 331.

¶ SCHENK (83), Plate 51, fig. 1.

** SAPORTA (94), p. 142.

†† WARD (96), p. 535.

‡‡ SAPORTA (94), Plate 22, figs. 9–11; Plate 26, figs. 17 and 18; Plate 27, figs. 1–5.

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

specimens have been omitted, and to avoid tedious discussion on questions of nomenclature, we have employed certain specific names in a wide sense, as indicating groups or series of forms which exhibit considerable variation, and may probably include types worthy of specific rank.

Name.	Record and Description of Species.	Geographical and Geological Distribution.	
DICTYOPHYLLUM.			
Dictyophyllum Nilssoni (BRONGN.) [including *D. acutilobum* (BRAUN.), *D. obtusifolium* (BRAUN.), *D. rugosum*, L. and H., *Thaumatopteris Muensteri*, GÖPP., *Camptopteris serrata*, SCHIMP. ex KURR MS.]	NATHORST (78), p. 14, Plate 1, fig. 14, Plate 4, figs. 6–8, Plate 5, Plate 6, figs. 2 and 3, Plate 7 (large specimen showing habit clearly).	Sweden (Scania).	Rhætic.
	NATHORST (86), p. 37, Plate 5, fig. 10, Plate 6, figs. 1–4, Plate 8, fig. 3, Plate 11, fig. 1.	,,	,,
	SCHENK (67), p. 75, Plate 16, fig. 1, p. 77, Plate 19, figs. 2–5, Plate 20, fig. 1.	Germany (Franconia).	,,
	BRAUNS (62), p. 54, Plate 13, fig. 11.	Germany.	,,
	SAPORTA (73), p. 325, Plate 34, fig. 2.	Vosges.	,,
	BARTHOLIN (94), p. 25, Plate 10, figs. 5 and 6.	Bornholm.	Jurassic.
	SCHENK (87), p. 5, Plate 2, fig. 7.	Persia.	Rhætic.
	SEWARD (00^2), p. 122, Plate 13, fig. 3, Plate 18, fig. 1, text-figs. 17–19. (List of synonyms and references given.)	England.	Jurassic.
	KRASSER (91), 9, 9.	Persia.	Rhætic.
	GÖPPERT (41), Lief. 192, Plates 1, 3 (figures of sporangia, and portions of large fronds).	Germany.	,,
	ZEILLER (82), p. 311, Plate 10, figs. 7 and 11.	Tong-King.	,,
	GERMAR (51), p. 119, Plate 14.	Quedlinburg.	Lower Cretaceous.
	POTONIÉ (99), p. 112, fig. 99.	Austria (Lunz).	Keuper.
	SCHIMPER (69), p. 632, Plate 42, fig. 4.	Germany (Stuttgart).	,,
Dictyophyllum platyphyllum (BRONGN.) (including *Propalmophyllum liasinum*, LIG., *Clathropteris meniscoides*, BRONGN.).	NATHORST (86), p. 41, Plate 6, fig. 6, Plate 7, fig. 2.	Sweden.	Rhætic.
	SCHENK (67), p. 81, Plate 16, figs. 2–9 (specimen showing sporangia), Plate 17 (unusually perfect fronds).	Germany (Franconia).	,,
	BRAUNS (62), p. 52, Plate 13, figs. 9 and 10.	Germany.	,,
	SAPORTA (73), p. 333, Plates 38–40.	France.	,,
	BARTHOLIN (94), p. 26, Plate 11, figs. 1–3.	Bornholm.	Jurassic.

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Name.	Record and Description of Species.	Geographical and Geological Distribution.	
	HEER (76), p. 72, Plate 25, figs. 2–6.	Switzerland.	Rhætic.
	SCHENK (83), p. 250, Plate 51, fig. 1.	China (Mongolia).	,,
	LIGNIER (95), p. 28, Plate 7, figs. 20 and 21. (ZEILLER* first pointed out the resemblance of Lignier's *Propalmophyllum* to *Clathropteris*).	France (Normandy).	Jurassic.
	ZEILLER (00), p. 116, fig. 89 (an exceptionally fine frond).	Tong-King.	Rhætic.
	FONTAINE (83), p. 54, Plate 31, figs. 3, 4, Plates 32–35.	North America (Virginia).	,,
	GÖPPERT (41), Lief. 5 and 6, Plates 18 and 19 (large frond).	Germany.	Jurassic.
	ZEILLER (82), p. 312, Plate 10, figs. 12 and 13, Plate 12, fig. 5.	Tong-King.	Rhætic.
	GERMAR (51), p. 117, Plate 16.	Quedlinburg (Germany).	Lower Cretaceous.
	HITCHCOCK (55), p. 22, fig. 2.	North America (Connecticut valley).	Rhætic.
	BRONGNIART (28), p. 380, Plate 134.	Vosges.	,,
CAMPTOPTERIS. *C. Spiralis*, NATH. (including *C. incisa*, NATH., and *C. serrata*, SCHIMP).	NATHORST (86), pp. 33, 35, 36, Plate 2, fig. 8, Plate 3, Plate 4, figs. 1–8, Plate 5, figs. 3–4, Plate 8, fig. 1.	Sweden (Scania).	,,
PROTORHIPIS. *Protorhipis Buchii*, AND. (including *P. Roemeri*, SCHENK, *Dictyophyllum cracoviense*, RAC., *D. Dicksoni*, HEER, *Hausmannia Forchhammeri*, BARTH.).	ANDRAE (53), p. 36, Plate 8, fig. 1.	Hungary.	Jurassic.
	ZEILLER (97), p. 50, Plate 21, figs. 1–5 (photographs of very good specimens).	,,	,,
	SEWARD (94), p. 140, figs. 16 and 17.	England.	Wealden.
	SCHENK (71), p. 224, Plate 31, fig. 3.	Germany.	,,
	SCHENK (75), Plate 27, fig. 8.		
	SEWARD (00), p. 18, Plate 3, fig. 34.	Belgium.	,,
	BARTHOLIN (94), p. 26, Plate 11, figs. 4–6, Plate 12, figs. 1 and 2.	Bornholm.	Jurassic.
	NATHORST (86), p. 57, Plate 11, figs. 2 and 4.	Sweden (Scania).	Rhætic.
	HEER (75), Plate 3, fig. 9.	Greenland.	Lower Cretaceous.
	RACIBORSKI (94), p. 47, Plate 14, figs. 5–10.	Poland.	Jurassic.
	POTONIÉ (00), p. 316.	Germany (Quedlinburg).	Lower Cretaceous.

* ZEILLER (97), p. 53.

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A small reniform leaf, described by ZIGNO, from the Jurassic rocks of Italy, as *Protorhipis asarifolia** may perhaps be correctly included in that genus, but its determination is open to question. A similarly and equally doubtful specimen has been described by HEER, from Siberia and Greenland, as *Protorhipis cordata.*† The reference to the occurrence of *Protorhipis* in the Neocomian beds of Quedlinburg, as stated by POTONIÉ, needs a word of explanation. In a short article in the "Naturwissenschaftliche Wochenschrift"‡ on Mesozoic ferns allied to *Dipteris*, POTONIÉ mentions, without figures or detailed description, some specimens from Quedlinburg, which he compares with small fronds of *Dipteris*; one of us had an opportunity of seeing these leaves in the Berlin Bergakademie, through the courtesy of Dr. POTONIÉ, and was struck by the close resemblance they bore to the *Protorhipis* fronds figured by ZEILLER from Hungary.§

The conclusion arrived at from a critical examination of the fossil records of the Dipteridinæ is that the genera *Dictyophyllum* and *Protorhipis* flourished most abundantly from the close of the Triassic to the beginning of the Cretaceous epoch. In Europe the Dipteridinæ were particularly vigorous in Scania during the Rhætic period, and they were represented, more or less abundantly, in the Rhætic and Jurassic vegetation of England, Germany, France, Belgium, Austria, Switzerland, Bornholm, Greenland, and Poland. The portions of large fronds figured by HITCHCOCK|| and more recently by FONTAINE¶ appear to afford good evidence for the existence of *Dictyophyllum* (*Clathropteris*) *platyphyllum*, in the North American continent, at the beginning of the Jurassic period. From Persia, and from the Far East, in Mongolia and Tong-King, traces of the Dipteridinæ have been recorded, but we know of no satisfactory examples from the plant-bearing strata of India, Africa, South America, or Australia. It is unfortunate that but few fronds of *Dictyophyllum* or *Protorhipis* have been found with clearly preserved sporangia. In their distribution and form the sori agree with those of *Dipteris*, but the annulus is described by GÖPPERT and others as probably complete; it is, however, admitted that the structure of the sporangia cannot be determined with certainty. We are still in want of information as to the anatomical characters of the fossil species, and our knowledge of the sporangia leaves much to be desired. The agreement between the recent species of *Dipteris* and the Mesozoic ferns referred to the Dipteridinæ, extends to the habit of the plant, the venation characters, and the form of the sori; it is, we believe, sufficiently striking to justify the inclusion of both the existing and extinct forms in the same family.

* ZIGNO (56), p. 176, Plate 23.
† HEER (82).
‡ POTONIÉ (00).
§ ZEILLER (97), Plate 21.
|| HITCHCOCK (55).
¶ FONTAINE (83).

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The genus *Matonia*, especially the species *M. pectinata*, R. Br.,* possesses certain features in common with *Dipteris*, and this resemblance extends to the fossil types of the Matonineæ and Dipteridinæ. The two recent species, *Matonia pectinata* and *Dipteris conjugata*, described by Wallace as growing side by side on the slopes of Mount Ophir, in the Malay Peninsula, agree in their habit of growth, in their long and creeping rhizomes characterised by the tubular form of the vascular tissue, and in the structural plan of their large and handsome fronds. Both *Matonia* and *Dipteris* exhibit points of contact with the Cyatheaceæ; and both differ from the typical Polypodiaceæ; both are characteristic ferns of the Malayan region at the present day, and in the early Mesozoic period representatives of the families Matonineæ and Dipteridinæ were among the most abundant and widely spread types in the European floras. The Mesozoic Matonineæ, with one or two possible exceptions,† appear to have been confined to Europe; the Dipteridinæ extended into Persia and the Far East and into North America, but there is no satisfactory evidence of their occurrence in the vegetation of Gondwana Land. These two genera, *Dipteris* and *Matonia*, in spite of differences in the nature of their sori and in the anatomy of their stems, are linked together as remnants from a bygone age, and exist as solitary survivals of a fern vegetation which has left abundant traces in the rocks of northern latitudes.

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* Seward (99).

† *E.g.*, Etheridge (90) has described a fragment of a fertile pinna of *Laccopteris* from Queensland.

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EXPLANATION OF PLATES.

(The microphotographs were taken by Mr. W. TAMS, Cambridge.)

PLATE 47.

DIPTERIS CONJUGATA.

Fig. 1. Portion of rhizome (nat. size).

Fig. 2. Portion of a more slender branched rhizome (nat. size).

Fig. 3. Transverse section of petiole. *t.* = secretory sacs (p. 496). (× 12.)

Fig. 4. Transverse section through the stele of a stem in the apical region, showing the foliar gap and the leaf-trace. *px.* = protoxylem (p. 497). (× 15.)

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Fig. 5. Transverse section of a young petiole near the base of the lamina (p. 498). (× 50.)

Fig. 6. Transverse section through the young stele of a stem near the separation of the leaf-trace (p. 498). (× 15.)

Fig. 7. Transverse section of part of the rhizome stele. *Rt.* = roots; *Rh.* = small tracheids at the point of origin of roots; *Px.* = protoxylem; *Ph.* = phloem; *Pc.* = pericycle; *e.* = endodermis (p. 494). (× 50.)

Fig. 8. Transverse section of rhizome—*pt.* = protophloem (p. 494). (× 15.)

Fig. 9. Transverse section of the outermost tissues of the rhizome, showing the bases of the ramenta (p. 493). (× 50.)

Fig. 10. Portion of lamina of a young frond, showing the venation and a few filamentous hairs (p. 495). (× 50.)

PLATE 48.

Dipteris conjugata, &c.

Fig. 11. Sporangium of *Dipteris Wallichii.* ⎫
Fig. 12. ,, ,, *D. Lobbiana.* ⎪
Fig. 13. ,, ,, *D. quinquefurcata.* ⎬ (P. 500.)
Fig. 14. ,, ,, *D. conjugata.* ⎪
Fig. 15. ,, ,, *D. conjugata.* ⎪
Fig. 16. ,, ,, *D. conjugata.* ⎭

Fig. 17. Part of frond of *D. conjugata.*

Fig. 18. *Dipteris quinquefurcata* (type-specimen in the Kew Herbarium).

Fig. 19. *Dipteris conjugata*—small frond ($\frac{1}{4}$ nat. size; Kew Herb.).

Fig. 20. *D. conjugata* ($\frac{1}{4}$ nat. size; British Museum Herb.).

Fig. 21. *D. Lobbiana* ($\frac{1}{4}$ nat. size; British Museum Herb.).

Fig. 22. *D. Wallichii* ($\frac{1}{4}$ nat. size; Kew Herb.).

Fig. 23. *D. conjugata* ($\frac{1}{4}$ nat. size; Kew Herb.).

Fig. 24. *D. Lobbiana*, var. *Ridleyi* (nat. size. From Dr. Christ, Basel).

PLATE 49.

Dipteris conjugata.

Fig. 25. Transverse section of meristele of petiole. *e.* = endodermis, *t.* = secretory sacs, *px.* = protoxylem (p. 497).

Fig. 26. Apex of rhizome. *r.* = ramenta, *d.* = desmogen strands (p. 493).

Fig. 27. Transverse section of young leaf. *v.* = veins (p. 496).

Fig. 28. Sieve-tube from the protophloem region of rhizome, showing sieve-areas (p. 494). (× 240.)

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Figs. 29 and 30. Ramenta (p. 493). (× 50.)

Fig. 31. Transverse section of meristele near base of the lamina (p. 498). *px.* = protoxylem, *e.* – *e'.* = inner and outer endodermis, *t.* = secretory sacs.

Fig. 32. Transverse section of stele of young rhizome. *pt.* = protophloem, *sv.* = sieve-plate (p. 494).

Fig. 33. Sorus; sporangia and glandular paraphyses (p. 490).

Fig. 34. Bases of ramenta, as seen in a section tangential to surface of the rhizome (p. 493).

Fig. 35. Diagram showing origin of leaf-trace (p. 499).

Fig. 36. Young ramenta (p. 493).

Fig. 37. Diagram showing branching of the rhizome stele (p. 494).

Fig. 38. Transverse section of a meristele in one of the main ribs of a leaf. *e* = endodermis, *f.* = fibres, *px.* = protoxylem, *pt.* = protophloem, *t.* = secretory sacs (p. 498).

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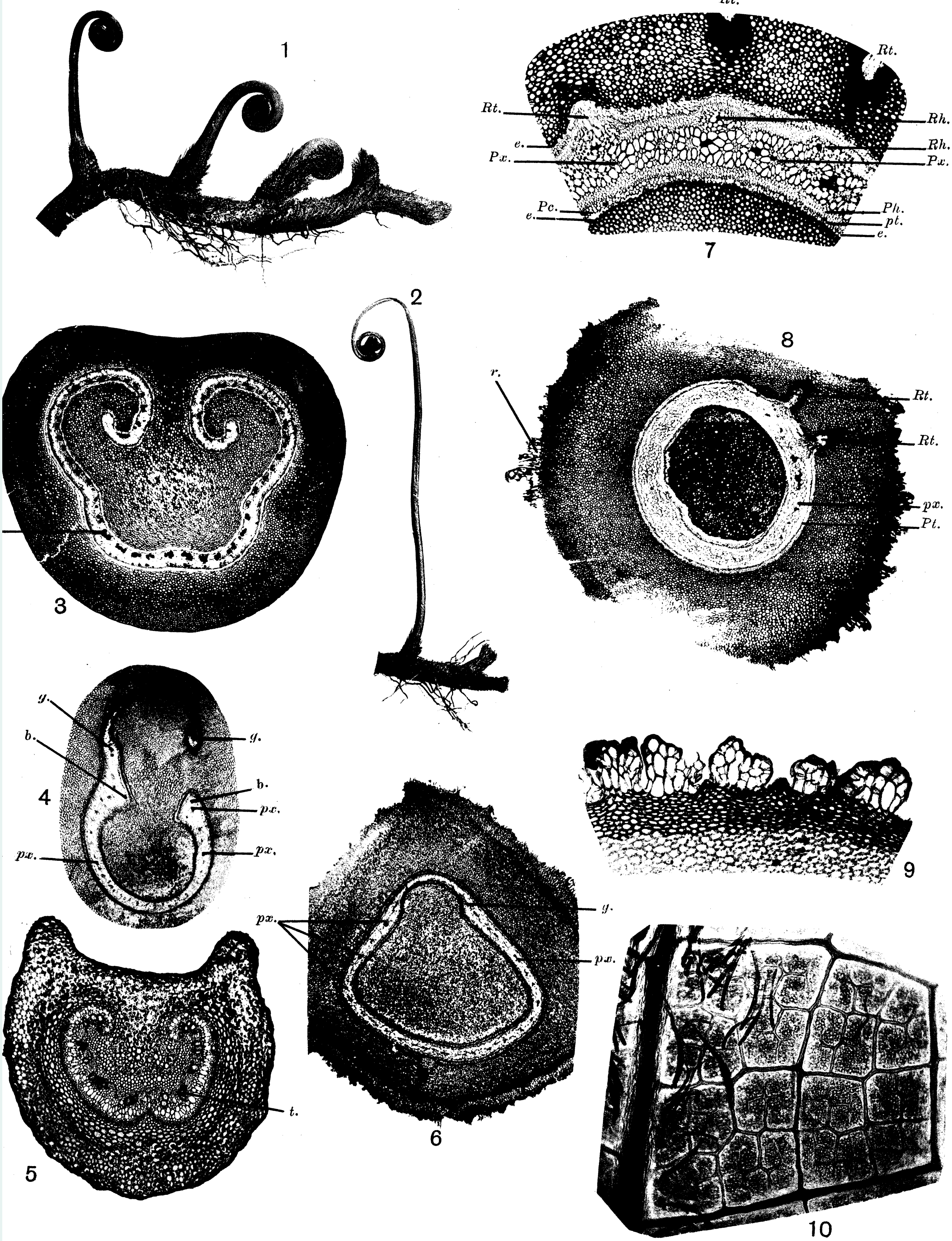

DIPTERIS CONJUGATA.

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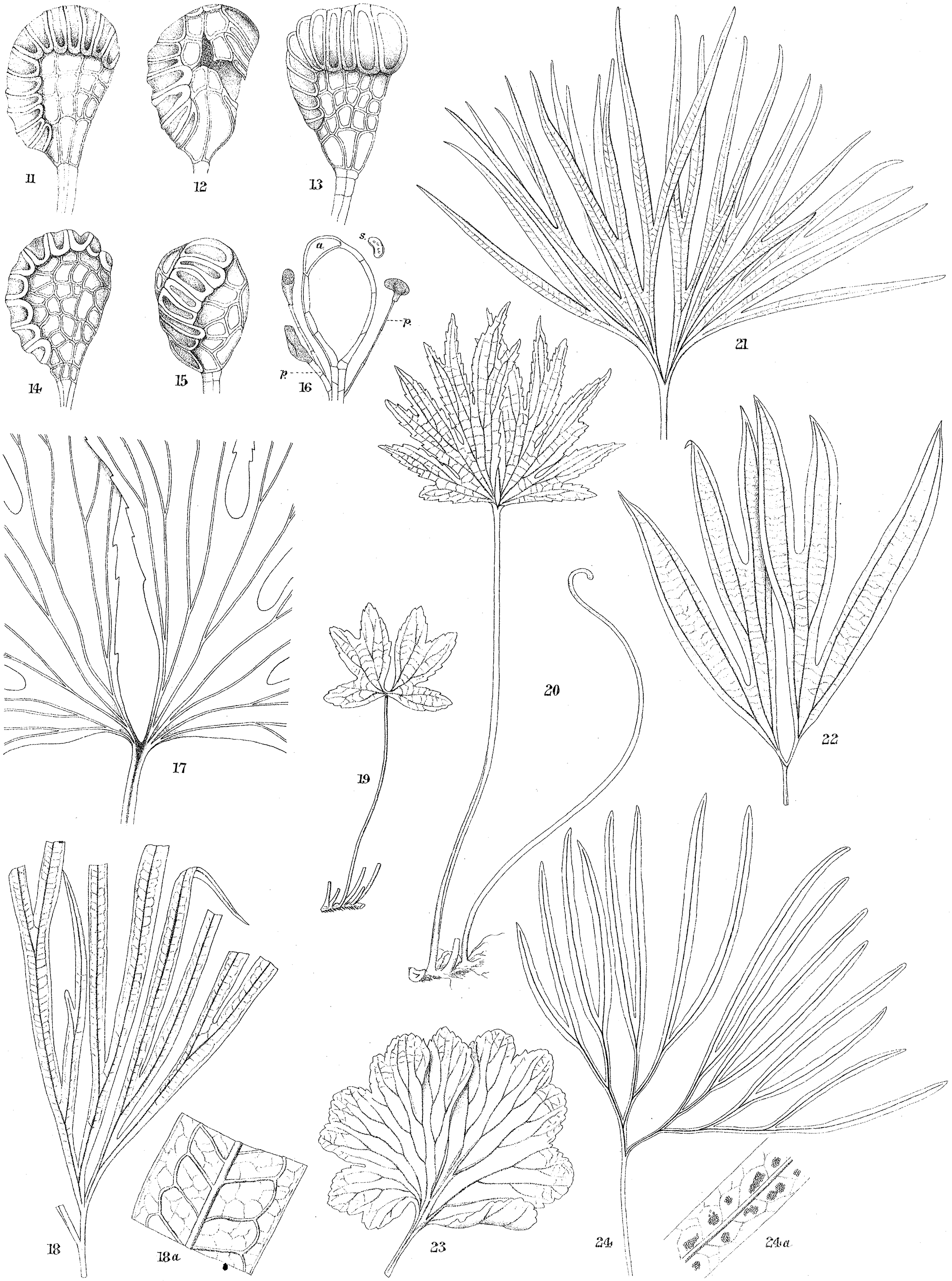

E. Dale del.
M. P. Parker lith.

Parker & West imp.

Dipteris.

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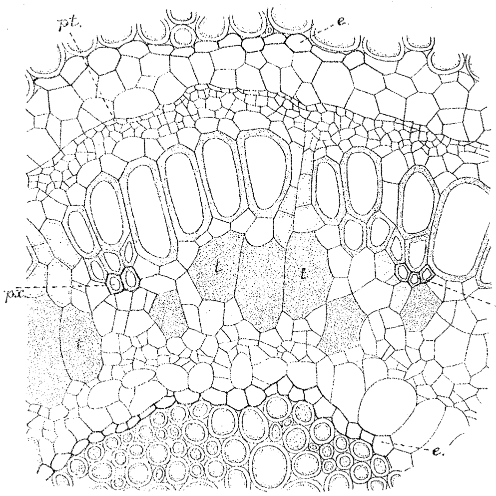

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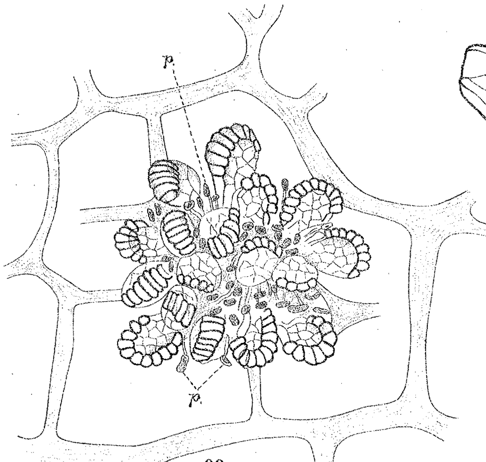

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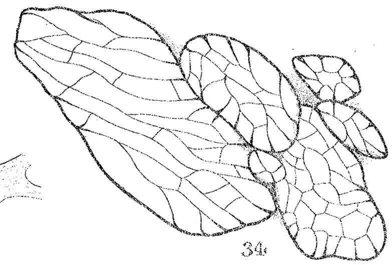
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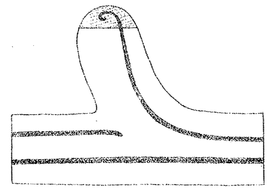
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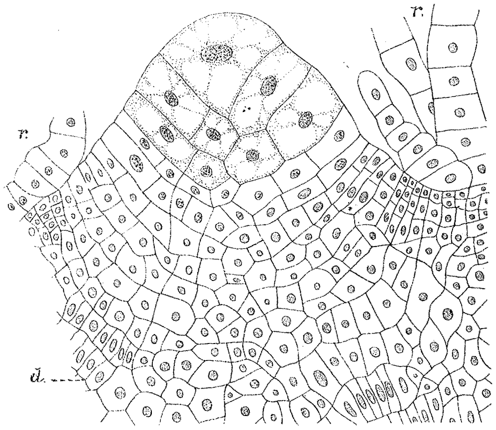

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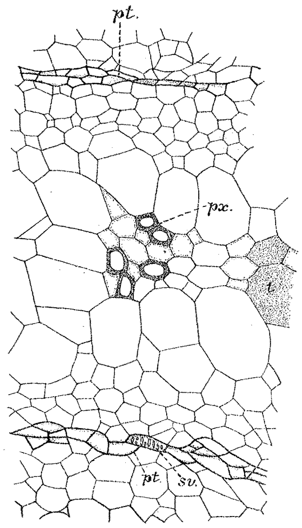

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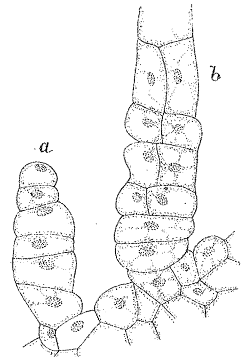

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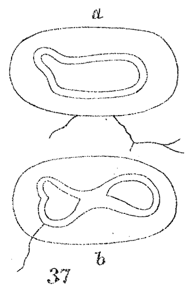

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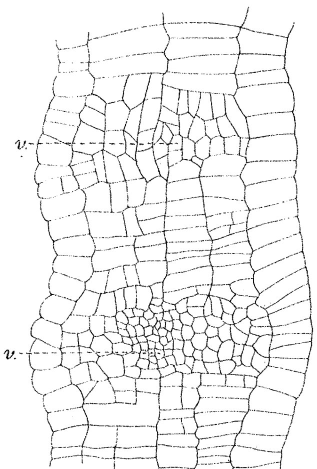

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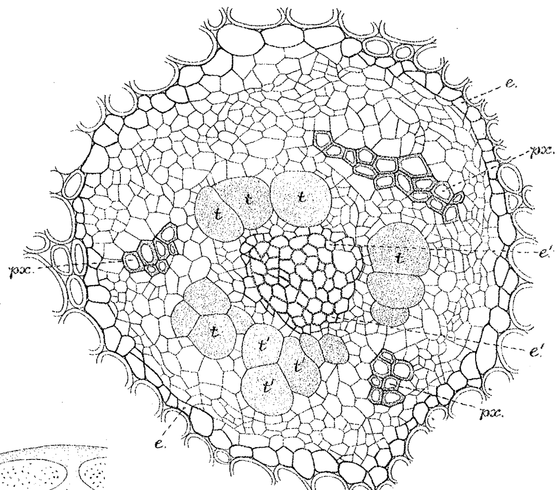

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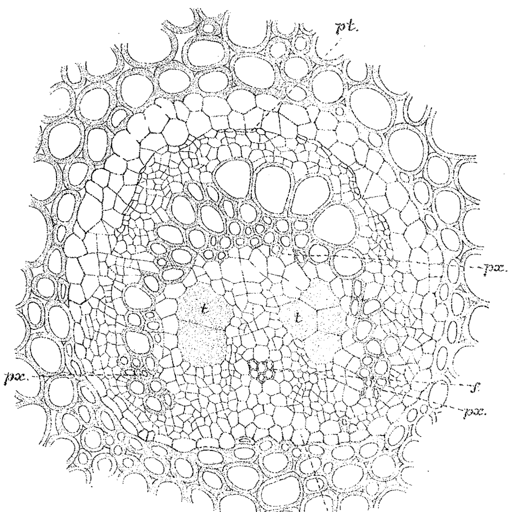

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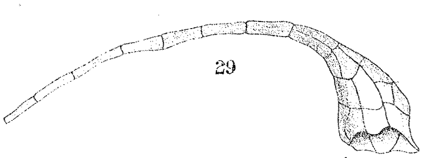
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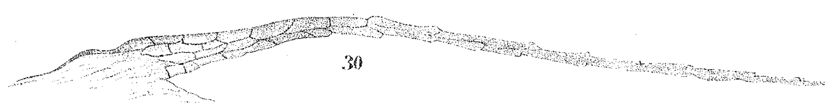
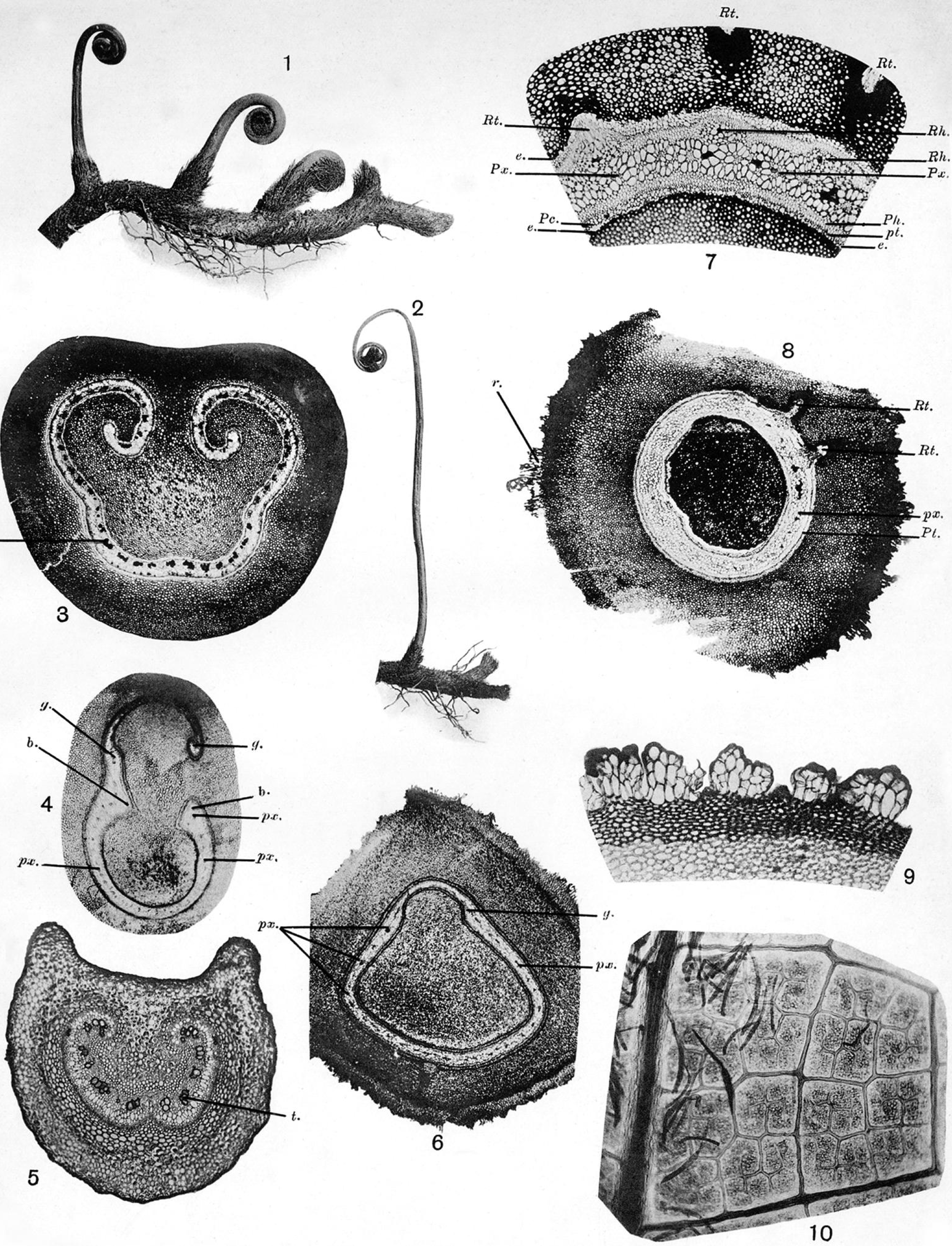

30

E. Dale del.
M. P. Parker lith.

Parker & West imp.

Dipteris conjugata.



DIPTERIS CONJUGATA.

PLATE 47.

DIPTERIS CONJUGATA.

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Fig. 1. Portion of rhizome (nat. size).

Fig. 2. Portion of a more slender branched rhizome (nat. size).

Fig. 3. Transverse section of petiole. *t.* = secretory sacs (p. 496). (× 12.)

Fig. 4. Transverse section through the stele of a stem in the apical region, showing the foliar gap and the leaf-trace. *px.* = protoxylem (p. 497). (× 15.)

Fig. 5. Transverse section of a young petiole near the base of the lamina (p. 498). (× 50.)

Fig. 6. Transverse section through the young stele of a stem near the separation of the leaf-trace (p. 498). (× 15.)

Fig. 7. Transverse section of part of the rhizome stele. *Rt.* = roots; *Rh.* = small tracheids at the point of origin of roots; *Px.* = protoxylem; *Ph.* = phloem; *Pc.* = pericycle; *e.* = endodermis (p. 494). (× 50.)

Fig. 8. Transverse section of rhizome—*pt.* = protophloem (p. 494). (× 15.)

Fig. 9. Transverse section of the outermost tissues of the rhizome, showing the bases of the ramenta (p. 493). (× 50.)

Fig. 10. Portion of lamina of a young frond, showing the venation and a few filamentous hairs (p. 495). (× 50.)

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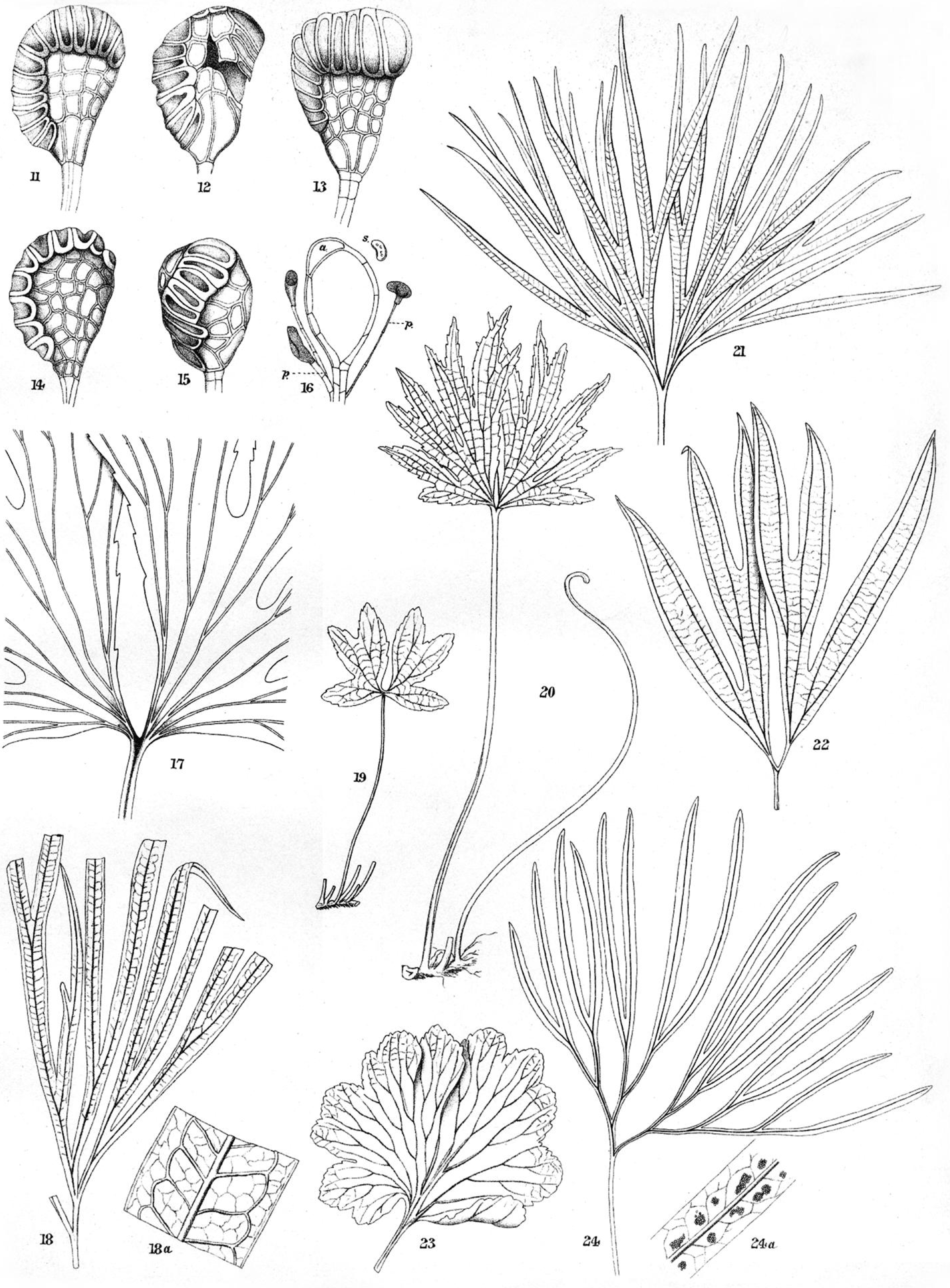

Dipteris.

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PLATE 48.

DIPTERIS CONJUGATA, &c.

Fig. 11. Sporangium of *Dipteris Wallichii.* ⎫
Fig. 12. ,, ,, *D. Lobbiana.* ⎪
Fig. 13. ,, ,, *D. quinquefurcata.* ⎬ (P. 500.)
Fig. 14. ,, ,, *D. conjugata.* ⎪
Fig. 15. ,, ,, *D. conjugata.* ⎪
Fig. 16. ,, ,, *D. conjugata.* ⎭
Fig. 17. Part of frond of *D. conjugata.*
Fig. 18. *Dipteris quinquefurcata* (type-specimen in the Kew Herbarium).
Fig. 19. *Dipteris conjugata*—small frond ($\frac{1}{4}$ nat. size; Kew Herb.).
Fig. 20. *D. conjugata* ($\frac{1}{4}$ nat. size; British Museum Herb.).
Fig. 21. *D. Lobbiana* ($\frac{1}{4}$ nat. size; British Museum Herb.).
Fig. 22. *D. Wallichii* ($\frac{1}{4}$ nat. size; Kew Herb.).
Fig. 23. *D. conjugata* ($\frac{1}{4}$ nat. size; Kew Herb.).
Fig. 24. *D. Lobbiana*, var. *Ridleyi* (nat. size. From Dr. CHRIST, Basel).

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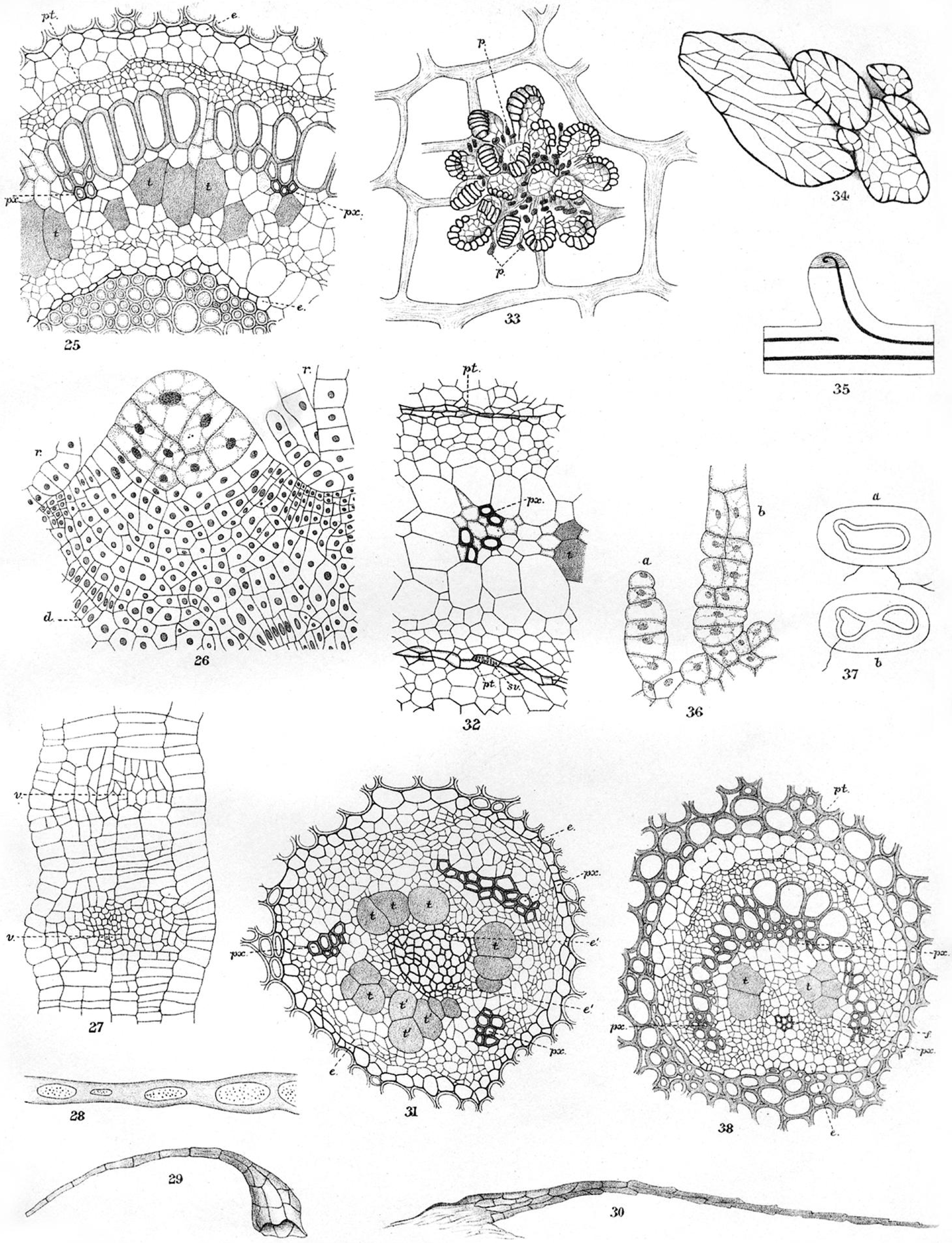

Dipteris conjugata.

PLATE 49.

Dipteris conjugata.

Fig. 25. Transverse section of meristele of petiole. *e.* = endodermis, *t.* = secretory sacs, *px.* = protoxylem (p. 497).

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Fig. 26. Apex of rhizome. *r.* = ramenta, *d.* = desmogen strands (p. 493).

Fig. 27. Transverse section of young leaf. *v.* = veins (p. 496).

Fig. 28. Sieve-tube from the protophloem region of rhizome, showing sieve-areas (p. 494). (× 240.)

Figs. 29 and 30. Ramenta (p. 493). (× 50.)

Fig. 31. Transverse section of meristele near base of the lamina (p. 498). *px.* = protoxylem, *e.* — *e'.* = inner and outer endodermis, *t.* = secretory sacs.

Fig. 32. Transverse section of stele of young rhizome. *pt.* = protophloem, *sv.* = sieve-plate (p. 494).

Fig. 33. Sorus; sporangia and glandular paraphyses (p. 490).

Fig. 34. Bases of ramenta, as seen in a section tangential to surface of the rhizome (p. 493).

Fig. 35. Diagram showing origin of leaf-trace (p. 499).

Fig. 36. Young ramenta (p. 493).

Fig. 37. Diagram showing branching of the rhizome stele (p. 494).

Fig. 38. Transverse section of a meristele in one of the main ribs of a leaf. *e* = endodermis, *f.* = fibres, *px.* = protoxylem, *pt.* = protophloem, *t.* = secretory sacs (p. 498).

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