

XI.—The Pinna-Trace in the Ferns. By R. C. Davie, M.A., B.Sc., late Robert Donaldson Research Scholar in the University of Glasgow, Lecturer in Botany in the University of Edinburgh. *Communicated by* Professor I. BAYLEY BALFOUR, F.R.S.

(MS. received May 4, 1914. Read June 1, 1914. Issued separately August 18, 1914.)

(Plates XXXIII.—XXXV.)

The relation of the leaf-trace to the vascular system of the stem in the Ferns has been exhaustively investigated during the past fifteen years by various workers, especially by GWYNNE-VAUGHAN and BOODLE in this country and by JEFFREY and his pupils in America. The interpretations of the numerous types of Fern stele and leaf-trace have caused much discussion. And the discovery of a wonderful series of fossil Ferns has not settled the discussion of the evolution of the Filicinean vascular system, but has carried the battle on to another field.

The fossils have recently yielded up the structure of their pinna-traces (KIDSTON, '08; BERTRAND, '09; GORDON, '11). Simultaneously an attack has been made on the pinna-traces of living Ferns. Various pinna-traces were described in curious mathematical formulæ, but no comparisons were made of the different types, by BERTRAND and CORNAILLE ('02) in their *Étude sur quelques caractéristiques de la structure des Filicinées actuelles*. TANSLEY in 1908 drew attention to the Fern leaf as the stronghold of many anatomical problems, and reproduced in detail almost the only account of the departure of the pinna-trace, that of *Matonia pectinata*, R. Br., by SEWARD ('99). COMPTON in 1909 described the branching of the leaf of *Matonia sarmentosa*, Baker, and figured the departure of the pinna-traces. CHRYSLER in 1910, in making comparisons among the Ophioglossaceæ, referred to pinna-traces in the Osmundaceæ and Polypodiaceæ, while SINNOTT in the same year described the pinna-traces of some of the Osmundaceæ. In 1911 SINNOTT made a rapid survey of the Filicinean leaf-traces, briefly referring to the relation between them and the pinna-traces. GWYNNE-VAUGHAN ('11) amplified some of the American work on the Osmundaceæ and made the first contribution to the knowledge of the pinna-trace in ontogeny. In 1912 BOWER described in detail the pinna-traces of *Lophosoria pruinata*, Pr., and *Gleichenia linearis* (Burm.) Clarke, and placed some weight upon the structure of the pinna-trace as a phyletic criterion. In working through the vascular anatomy of *Peranema cyatheoides*, D. Don, I found a difference in the type of pinna-trace departure in the basal and terminal pinnæ, and, following the lead of CHRYSLER ('10, p. 5), named the one "extramarginal" and the other "marginal" (DAVIE, '12).

In the marginal type the first indication of the preparation for the departure of

the pinna-trace, as the leaf-trace is followed up the petiole, is an extension of the mass of tracheides on the adaxial side of the petiole. In *Asplenium obtusatum*,* Forst. (Pl. XXXIII. fig. 1), which may serve as an example of this type, the two masses of xylem are curved in outline, the convex sides of the curves being directed towards each other. The adaxial extremities of these xylem-masses become extended towards the adaxial corners of the petiole. As the pinnæ are not inserted exactly opposite to each other, first the extremity of one and then that of the other xylem-mass is separated off from the parent trace. Phloem completely surrounds the xylem in both portions of the leaf-trace, and the marginal tracheides when nipped off are surrounded by a narrow ring of phloem. There are protoxylem elements at the abaxial tips of the leaf-trace and on the adaxial sides, not far from the ends. The pinna-trace has one small protoxylem group on one side at the time of separation.

As the tracheides at the margin of the leaf-trace strand are separated from the parent strand to supply the pinna-trace, this type of pinna-supply is termed the "marginal" one.

The marginal type is not always as simple as this, however. In *Loxsonia Cunninghami*, R. Br. (Pl. XXXIII. figs. 5 and 6), the leaf-trace in the base of the petiole is curved in outline. It has a little hook at each extremity. Below the first pinna this trace extends laterally; the hook is pushed further and further from the centre of the petiole, a widening of the leaf-trace takes place in the antero-posterior direction just back from the hooked extremity (Pl. XXXIII. fig. 5); this widened region becomes arched like the parent trace, and the arched extremity is nipped off as a pinna-trace (Pl. XXXIII. fig. 6).

This is more complicated than the process in *Asplenium obtusatum*, the presence of the hooked extremities dictating the complexity.

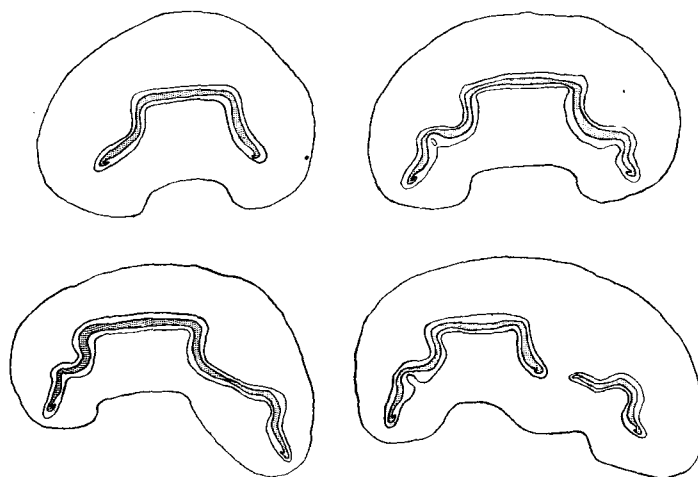
In *Balanium culcita* (L'Hérit.) Klf. (Pl. XXXIV. fig. 13) the leaf-trace has small terminal hooks. Its outline is at first that of a simple arch with an almost flat abaxial portion flanked by curves (text-fig. 1). As the trace ascends towards the first pinnæ it becomes extended towards the adaxial corners of the petiole; an arching more marked than that of *Loxsonia* goes on in the extensions, and the pinna-trace departs as a replica of the parent trace, taking with it the original margin.

The simplest example of the marginal type of supply from a hooked leaf-trace is found in *Aneimia hirta* (L.) Sw. (Pl. XXXIII. fig. 3). Each hook is merely a little group of tracheides placed at right angles to the set composing the side of the leaf-trace. The pinna is supplied from an extension of the extremity in the usual manner. A swelling in the side of the leaf-trace not far from the tip is the breaking-point for the pinna-trace. The new hook of the leaf-trace is the remnant of the dilated portion.

All four types agree in nipping off the margins of the leaf-traces to supply the pinnæ.

* For the sake of uniformity, the nomenclature throughout this paper is that of the *Index Filicum* (CHRISTENSEN, 1906).

The "extramarginal" types differ from them in leaving the leaf-trace margins intact throughout the petiole. In *Didymochlæna truncatula* (Sw.) J. Sm. (Pl. XXXIII. fig. 7), the leaf-trace is composed of several strands. The two adaxial strands have their margins sharply recurved, so that they are almost parallel to the adaxial surface of the petiole. To supply the basal pinna, the back of the hook is lengthened towards the adaxial corner of the petiole. Across the narrow space between the two strips of tracheidal tissue thus formed new tracheides spread. The original outline of the leaf-trace strand is thus re-formed, while a ring of tracheides is attached to the back of its hooked portion. This ring soon separates, to pass into the base of the pinna and divide up into a pinna-trace resembling the leaf-trace. The margin of



TEXT-FIG. 1. —*Balantium culcita* (L'Hérit.) Klf. Successive stages in the development and liberation of the pinna-trace.

the parent trace remains intact during the process. Since the pinna-trace goes off from the outside of the parent strand, the method of supply may be termed "extramarginal."

The process of supplying the basal pinnæ is exactly the same in leaves with unbroken leaf-traces, such as that of *Odontosoria chinensis* (L.) J. Sm., var. *Veitchii* (Pl. XXXIV. fig. 9).

In this species and in *Didymochlæna truncatula* no gaps are left in the tissues of the parent trace when the pinna-trace is given off. Sometimes, however, the departure of the pinna-trace makes a gap in the tissues at the back of the hook in the leaf-trace. This is readily seen in *Leptopteris hymenophylloides* (A. Rich.) Pr. (Pl. XXXIII. fig. 8). *Hymenophyllum demissum* (Forst.) Sw. (Pl. XXXIV. fig. 10) gives off the supply to the basal pinnæ in the extramarginal manner. The tracheides of the leaf-trace do not form a perfectly continuous series, but the marginal set, which terminate the hook of the leaf-trace, remain in position when the pinna-trace departs. It can hardly be said that a gap occurs opposite to the departing pinna-trace, for a single tracheide occurs between the end of the abaxial curve and the

marginal set of tracheides. The method of pinna-supply in *Blechnum orientale*, L. (Pl. XXXIV. fig. 11), is the most nearly marginal among the extramarginal types. Only one or two of the marginal tracheides remain when the pinna-trace departs, but the method of separation of the pinna-trace is certainly extramarginal. The typical lengthening of the hook, the bridging of the narrow space between the adaxial curve and the margin of the hook, and the retention of the marginal tracheides are all found in the process in this Fern.

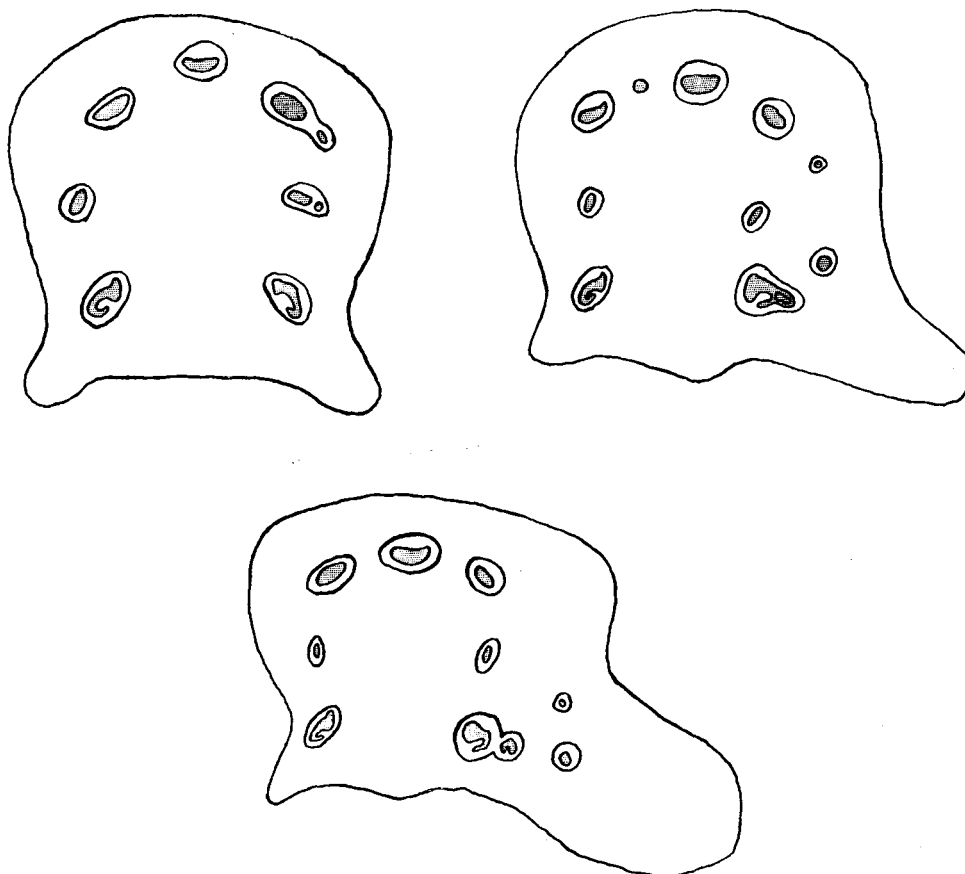
"Thin partitions" divide the bounds of marginal and extramarginal types. *Gymnogramma Pearcei*, Moore, var. *robusta* (Pl. XXXIV. fig. 12), *Ceropteris calomelanos* (L.) Und., and *C. calomelanos*, var. *chrysophylla*, Klf., have the same type of leaf-trace strand as *Blechnum orientale*. The pinna-trace goes off from a lengthened leaf-trace strand, which, however, re-forms its hooked extremity from a swelling of tracheides back from the margin. This swelling never catches up the marginal set of tracheides of the original leaf-trace. The *Gymnogramma* type is but a step from the type described in *Blechnum orientale*.

Histiopteris incisa (Thbg.) J. Sm. (Pl. XXXIV. fig. 15 and Pl. XXXV. fig. 16) illustrates a curious combination of the two types in its process of pinna-supply. The leaf-trace has the outline of that of *Balantium culcita*—a flat-topped arch with incurved sides. Small hooks are present at its extremities. The hooked extremity lengthens in the usual way and gives off its tip in marginal fashion. Simultaneously the projecting corner of the arch beside it also lengthens, and from it is nipped off a ring of vascular tissue in the extramarginal manner (Pl. XXXIV. fig. 15). The two strands pass towards the base of the pinna, come together, and by the opening out of the adaxial side of the extramarginally-derived portion form a pinna-trace exactly like the leaf-trace (Pl. XXXV. fig. 16).

In one or two broken leaf-traces a reminiscence of this combined process seems to appear. All three strands are unhooked in *Aspidium Moorei* (Hk.) Diels. Part of the pinna-trace comes from the tip of the adaxial strand, part from the median strand—those parts which correspond to tip and arch-corner in *Histiopteris incisa*. The pinna-trace of *Leptochilus cuspidatus* (Pr.) C. Chr. also comes from portions of the leaf-trace corresponding to those supplying the pinna in *Histiopteris incisa*. The leaf-trace is made up of six or seven strands (text-fig. 2). The adaxial pair have incurved extremities and give off the backs of their hooks to supply part of the pinna-trace. The rest of the pinna-trace comes from the two subsidiary strands next in order to the adaxial strand as we go towards the abaxial side of the petiole. These subsidiary strands have simple plates of xylem, from which the strands going to the pinnæ are simply nipped off.

The pinna-traces of most of the Cyatheaceæ bear a resemblance to these. GWYNNE-VAUGHAN ('03) has called attention to the distinction made by BERTRAND and CORNAILLE ('02) between the two regions of the petiolar trace, (1) the abaxial curve, and (2) the adaxial arcs. The pinna-trace of *Cyathea Brunonis* comes partly

"from the point where the adaxial arc or the xylem hook joins on to the abaxial curve," and partly "from the abaxial curve itself at the point where it is folded inwards." These are just the points of departure of the pinna-trace in *Histiopteris incisa* and *Leptochilus cuspidatus*, but the involution of the trace in *Cyathea Brunonis* and its folding to the abaxial curve make both strands in it go off extra-marginally.



TEXT-FIG. 2.—*Leptochilus cuspidatus* (Pr.) C. Chr., showing the method of pinna-supply from the leaf-trace.

These types of pinna-trace cover the variations which are found in the genera examined. Upwards of a hundred and fifty species have been worked through, and the method of vascular supply to all the pinnæ noted from base to apex of the leaf. The species were at first chosen at random, but soon a general trend could be observed through the families in phyletic order. And the later species examined were selected because of their positions on phyletic lines. The classification adopted in the accompanying table of the results (p. 354) is that of DIELS in ENGLER and PRANTL'S *Natürliche Pflanzenfamilien*, a classification which corresponds closely to BOWER'S grouping into Simplicēs—Gradatæ—Mixtæ.

Starting with the Leptosporangiate Ferns, we have the Osmundaceæ showing extramarginal supply to the pinna-traces. The length of the gap may vary. It is

Summary of Results of Investigation.

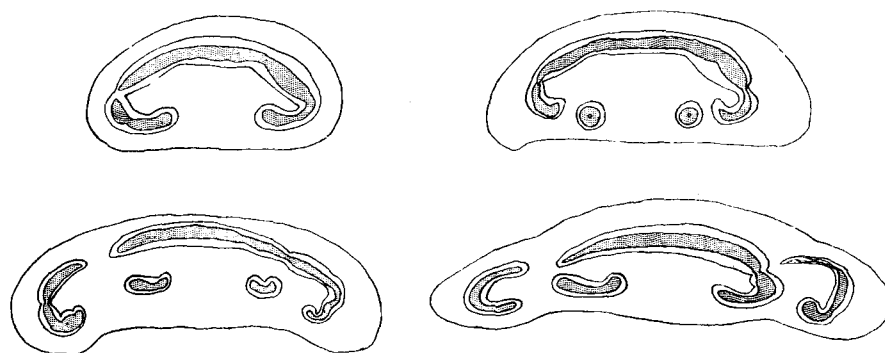
Family.	Marginal Type of Pinna-Supply.	Extramarginal Type of Pinna-Supply.
Schizaeaceæ	<i>Lygodium circinnatum</i> (Burm.) Sw.; <i>L. scandens</i> (L.) Sw. <i>Mohria caffrorum</i> (L.) Desv. <i>Aneimia collina</i> , Raddi; <i>A. hirta</i> (L.) Sw.; <i>A. phyllitidis</i> (L.) Sw.; <i>A. rotundifolia</i> , Schrad.	...
Osmundaceæ	...	<i>Todea barbara</i> (L.) Moore. <i>Leptopteris hymenophylloides</i> (A. Rich.) Pr. <i>Osmunda javanica</i> , Bl.; <i>O. regalis</i> , L.
Gleicheniaceæ	...	<i>Gleichenia circinnata</i> , Sw., var. <i>speluncæ</i> ; <i>G. flabellata</i> , R.Br.; <i>G. rupestris</i> , R.Br.
Hymenophyllaceæ	...	<i>Hymenophyllum demissum</i> (Forst.) Sw.; <i>H. dilatatum</i> (Forst.) Sw. <i>Trichomanes elegans</i> , Rich.; <i>T. radicans</i> , Sw.
Loxsomaceæ	<i>Loxsonia Cunninghami</i> , R.Br.	...
Cyatheaceæ	<i>Balanium culcita</i> (L'Hérit.) Klf. <i>Dicksonia fibrosa</i> , Col.	<i>Cibotium Schiedei</i> , Schlecht. et Cham. <i>Thyrsopteris elegans</i> , Kze. <i>Cyathea mexicana</i> , Schlecht. et Cham.; <i>C. pubescens</i> , Mett. <i>Hemitelia grandifolia</i> (Willd.) Spr. <i>Alsophila glauca</i> (Bl.) J. Sm.
Woodsieæ	<i>Cystopteris fragilis</i> (L.) Bernh.; <i>C. montana</i> (Lam.) Bernh.	<i>Peranema cyatheoides</i> , Don. <i>Diacalpe aspidioides</i> , Bl. <i>Woodsia ilvensis</i> (L.) R.Br.; <i>W. polystichoides</i> , Eat. <i>Matteucia orientalis</i> (Hk.) Trev.; <i>M. struthiopteris</i> (L.) Todaro. <i>Onoclea sensibilis</i> , L.
Aspidieæ	...	<i>Dryopteris filix mas</i> (L.) Schott.; <i>D. phegopteris</i> (L.) C. Chr.; <i>D. pulvinulifera</i> (Bedd.) O. Ktze.; <i>D. serrata</i> (Cav.) C. Chr.; <i>D. setigera</i> (Bl.) O. Ktze. <i>Didymochlæna truncatula</i> (Sw.) J. Sm. <i>Polystichum aculeatum</i> (L.) Schott., var. <i>angulare</i> , Pr.; <i>P. Standishii</i> (Moore) C. Chr.
Davalliæ	<i>Nephrolepis Amerpohlil</i> , hort.; <i>N. Fosteri</i> , hort., Hill; <i>N. Pieroni</i> , hort.; <i>N. Scottii</i> , hort. <i>Humata repens</i> (L. fil.) Diels, var. <i>alpina</i> . <i>Microlepia hirsuta</i> (J. Sm.) Pr. <i>Lindsaya repens</i> (Bory) Bedd. <i>Odontosoria retusa</i> (Cav.) J. Sm. <i>Davallia assamica</i> (Bedd.) Bak.; <i>D. bullata</i> , Wall.; <i>D. dissecta</i> , J. Sm.; <i>D. immersa</i> , Wall.; <i>D. pallida</i> , Mett.; <i>D. pentaphylla</i> , Bl.; <i>D. solida</i> (Forst.) Sw.; <i>D. solida</i> , var. <i>hijiensis</i> .	<i>Leptolepia novæ-zelandiæ</i> (Col.) Kuhn. <i>Microlepia hirta</i> (Klf.) Pr.; <i>M. hirta</i> , var. <i>cristata</i> ; <i>M. platyphylla</i> (Don), J. Sm.; <i>M. speluncæ</i> (L.) Moore; <i>M. strigosa</i> (Thbg.) Pr. <i>Dennstaedtia adiantoides</i> (H. B. Willd.) Moore. <i>Odontosoria chinensis</i> (L.) J. Sm., var. <i>Veitchii</i> .
Asplenieæ	<i>Asplenium adiantum nigrum</i> , L.; <i>A. bulbiferum</i> , Forst., var. <i>Fabianum</i> ; <i>A. bulbiferum</i> , var. <i>Hillii</i> ; <i>A. obtusatum</i> , Forst.; <i>A. præmorsum</i> , Sw.; <i>A. ruta-muraria</i> , L.; <i>A. tenerum</i> , Forst. <i>Ceterach officinarum</i> , DC.	<i>Blechnum attenuatum</i> (Sw.) Mett.; <i>B. brasiliense</i> , Desv.; <i>B. capense</i> (L.) Schlecht.; <i>B. discolor</i> (Forst.) Keys.; <i>B. Moorei</i> , C. Chr.; <i>B. tabulare</i> (Thbg.) Kuhn; <i>B. Banksii</i> (Hk. fil.) Mett.; <i>B. lanceolatum</i> (R.Br.) Sturm; <i>B. Patersoni</i> (R.Br.) Mett.; <i>B. occidentale</i> , L.; <i>B. orientale</i> , L. <i>Doodia aspera</i> , R.Br., var. <i>multifida</i> . <i>Brainea insignis</i> (Hk.) J. Sm. <i>Athyrium filix femina</i> (L.) Roth. <i>Diplazium celtidifolium</i> , Kze.; <i>D. marginatum</i> (L.) Diels. <i>Woodwardia radicans</i> (L.) Sm.
Pterideæ	<i>Gymnogramma Pearcei</i> , Moore, var. <i>robusta</i> . <i>Ceropteris calomelanos</i> (L.) Und.; <i>C. calomelanos</i> , var. <i>chrysophylla</i> , Klf. <i>Pellaea hastata</i> (Thbg.) Prantl; <i>P. rotundifolia</i> (Forst.) Hk. <i>Cryptogramma crispa</i> (L.) R.Br. <i>Cheilanthes argentea</i> (Gmel.) Kze.; <i>C. myriophylla</i> , Desv., var. <i>elegans</i> . <i>Notholæna affinis</i> (Mett.) Moore; <i>N. bonariensis</i> (Willd.) C. Chr. <i>Pteris biaurita</i> , L.; <i>P. cretica</i> , L.; <i>P. umbrosa</i> , R.Br.	<i>Trimeria trifoliata</i> (L.) Diels. <i>Adiantum polyphyllum</i> , Willd.; <i>A. sanctæ catherinæ</i> , hort., J. Sm. <i>Notholæna sinuata</i> (Lag.) Klf.
Polypodieæ	<i>Polypodium aureum</i> , L.; <i>P. brasiliense</i> , Poir.; <i>P. phymatodes</i> , L.; <i>P. Schneideri</i> , hort., Veitch; <i>P. vulgare</i> , L. <i>Drynaria rigidula</i> (Sw.) Bedd.	...

long in *Leptopteris hymenophylloides* and in *Osmunda javanica*, Bl., quite short in *O. regalis*, L. The pinna-traces of *Leptopteris hymenophylloides* and *Osmunda regalis* are wide; those of *Todea barbara* (L.) Moore and *O. javanica* are narrow.

The Schizæaceæ, in contrast, invariably supply their pinnæ in the marginal fashion. In *Lygodium circinnatum* (Burm.) Sw. and *L. scandens* (L.) Sw., the leaf-trace is unincurved and the supply is quite directly marginal. It is so also in *Mohria caffrorum* (L.) Desv. The hooked leaf-trace already described for *Aneimia hirta* is found also, though less prominently, in *Aneimia collina*, Raddi (Pl. XXXIII. fig. 4), while slight hooks also appear in *A. phyllitidis* (L.) Sw. and *A. rotundifolia*, Schrad.

In all of these the pinna-trace goes off marginally.

The third family of the Simplices—the Gleicheniaceæ—is consistently extra-marginal in supplying its pinnæ. BOODLE ('01) and BOWER ('12) have described the



TEXT-FIG. 3.—*Gleichenia flabellata*, R. Br. Diagrammatic representation of the changes occurring in the vascular system of the petiole during the liberation of the pinna-traces.

pinna-traces of *Gleichenia dicarpa*, R. Br., var. *longipinnata*, *G. flabellata*, R. Br., and *G. linearis* (Burm.) Clarke. In *Gleichenia flabellata* (Pl. XXXIV. fig. 14) the incurved margins become nipped off from the rest of the leaf-trace on its inner side, round themselves into little rings of tracheides, and run up isolated from the main part of the trace for some distance. The back of the remaining hook separates off to go to the pinna, and then these isolated circles open out on their abaxial sides and re-form the leaf-trace by extending to meet its margins (text-fig. 3). In *Gleichenia rupestris*, R. Br., the margins of the leaf-trace separate off when the pinna-traces are being given off, but here they do not form two rings but only a couple of arcs with the concave sides towards the centre of the petiole. They may even become attached to each other by their margins. In *Gleichenia circinnata*, Sw., var. *speluncæ*, the pinna-supply is of the normal extramarginal type; almost no gap occurs in the tissues of the leaf-trace when the pinna-trace is given off.

The method of supply in *Gleichenia flabellata* and *G. rupestris* may be regarded as a special variety of the type seen in the Osmundaceæ, as long gaps are thus formed in the leaf-trace opposite to each pinna.

Passing to the Gradatæ, we find the extramarginal type prevails. In the

Hymenophyllaceæ it occurs in *Hymenophyllum demissum*, *H. dilatatum* (Forst.) Sw., *Trichomanes elegans*, Rich., and *T. radicans*, Sw.

A divergence into the marginal type occurs in *Loxsonia Cunninghamsi*, described above, while the type of *Balantium culcita* is repeated among the Cyatheaceæ in *Dicksonia fibrosa*, Col. In the other members of the Cyatheaceæ examined the extramarginal type prevails. These include *Cibotium Schiedei*, Schlecht. et Cham., *Thyrsopteris elegans*, Kze., *Cyathea mexicana*, Schlecht. et Cham., *C. pubescens*, Mett., *Hemitelia grandifolia* (Willd.) Spr., and *Alsophila glauca* (Bl.) J. Sm.

Passing into the Ferns on the border-line between Gradatæ and Mixtæ, we have the broken leaf-trace in *Peranema cyatheoides*, Don, and *Diacalpe aspidioides*, Bl., the unbroken leaf-trace in *Woodsia ilvensis* (L.) R. Br., *W. polystichoides*, Eat., *Matteucia orientalis* (Hk.) Trev., *M. struthiopteris* (L.) Todaro, and *Onoclea sensibilis*, L. (in the last three the leaf-trace is binary at its departure from the stalk, but unbroken below the pinnæ). In all of these the pinna-trace goes off extramarginally from the back of the hook, whether in the unbroken trace or in the adaxial strand of the broken type.

In the genus *Cystopteris* there is a variation; in *Cystopteris fragilis* (L.) Bernh. and *C. montana* (Lam.) Bernh., the supply to the pinnæ is marginal. The leaf-traces have slightly hooked ends to each portion of the binary strands. The whole set of tracheides lengthens, a "thickening" of the number occurs about the centre of the leaf-trace on the adaxial face, a break takes place there in the series, and the "daughter" trace separates off. Below the second pair of pinnæ the binary trace becomes an unbroken strand, and the supply is there distinctly marginal. The supply to the basal pinnæ resembles the type already described for some species of *Gymnogramma* and *Ceropteris* (p. 352), though the thickening is less marked in *Cystopteris*.

In the Aspidiæ, the leaf-traces are of the broken type and the supply to the pinnæ is extramarginal. In *Dryopteris phegopteris* (L.) C. Chr. there is a gap opposite to the pinna. In *Dryopteris pulvinulifera* (Bedd.) O. Ktze., *D. filix mas* (L.) Schott, *D. setigera* (Bl.) O. Ktze., *D. serrata* (Cav.) C. Chr., *Didymochlæna truncatula*, *Polystichum aculeatum* (L.) Schott, var. *angulare*, Pr., *P. Standishii* (Moore) C. Chr., the supply is extramarginal. In *Aspidium Moorei* (see above, p. 352), the pinna-trace comes partly, marginally, from the tip of the adaxial strand, and partly from the median strand of the leaf-trace.

From the Aspidiæ forwards into the main mixed Ferns both extramarginal and marginal types of pinna-supply occur. The Davalliæ carry forward the extramarginal type through *Leptolepia novæ-zelandiæ* (Col.) Kuhn, *Microlepia hirta* (Klf.) Pr., *M. hirta*, var. *cristata*, *M. speluncæ* (L.) Moore, *M. platyphylla* (Don) J. Sm., *M. strigosa* (Thbg.) Pr., and *Dennstaedtia adiantoides* (H. B. Willd.) Moore. *Microlepia hirsuta* (J. Sm.) Pr., *Nephrolepis Amerpohlii*, hort., *N. Fosteri*, hort., Hill, *N. Piersoni*, hort., and *N. Scottii*, hort., all distinctly show the marginal type. *Humata repens* (L. fil.) Diels, var. *alpina*, and *Lindsaya repens* (Bory) Bedd., are

also marginal. In the genus *Odontosoria* both types appear. *Odontosoria chinensis*, var. *Veitchii* (see above, p. 351), is pronouncedly extramarginal, but *O. retusa* (Cav.) J. Sm. is marginal. The marginal type occurs in *Davallia assamica* (Bedd.) Bak., *D. bullata*, Wall., *D. dissecta*, J. Sm., *D. immersa*, Wall., *D. pallida*, Mett., *D. pentaphylla*, Bl., *D. solida* (Forst.) Sw., and *D. solida*, var. *fijiensis*.

This appearance of both types in a number of species within a family is repeated again in the Asplenieæ; but in them the extramarginal type is restricted to certain genera, the marginal type to others.

A marked and consistent adherence to the extramarginal type is found in the genera *Blechnum*, *Doodia*, *Woodwardia*, and *Brainea*. In *Blechnum attenuatum* (Sw.) Mett., *B. brasiliense*, Desv., *B. capense* (L.) Schlecht., *B. discolor* (Forst.) Keys., *B. Moorei*, C. Chr., *B. tabulare* (Thbg.) Kuhn, *Doodia aspera*, R. Br., var. *multifida*, and *Brainea insignis* (Hk.) J. Sm., the type of supply is like that seen in *Didymochlæna truncatula*, the pinna-trace departing from the back of a very distinctly incurved adaxial leaf-trace bundle.

An even more pronounced form of the extramarginal type is found in *Woodwardia radicans* (L.) Sm., where the large pinna-trace arches up almost before it is free from the parent bundle, and then breaks into several separate strands.

In *Blechnum Banksii* (Hk. fil.) Mett., *B. lanceolatum* (R. Br.) Sturm, and *B. Patersoni* (R. Br.) Mett., the adaxial leaf-trace bundles are short and narrow, and the number of tracheides in the hooked ends is quite small. The pinna-trace is undoubtedly extramarginal, though only a few tracheides of the margin are left when it has gone off. *Blechnum occidentale* (L.) is also extramarginal, but approaches very closely to *B. orientale*, which is only just extramarginal.

The other extramarginal members of the Asplenieæ are *Athyrium filix femina* (L.) Roth., *Diplazium celtidifolium*, Kze., and *D. marginatum* (L.) Diels, in which the large pinna-traces go off from the back of wide leaf-traces with distinct terminal hooks. The amount left of the original margin after the leaf-trace has gone off is greater in *Athyrium filix femina* and *Diplazium marginatum* than in *Diplazium celtidifolium*.

In the genus *Asplenium* the supply is consistently marginal. In *Asplenium bulbiferum*, Forst., var. *Fabianum*, and in *A. bulbiferum*, var. *Hillii*, *A. adiantum nigrum* (L.), *A. præmorsum*, Sw., *A. obtusatum*, *A. tenerum*, Forst., and *A. rutamuraria* (L.), species which differ from one another in size of leaf, in complexity of leaf-segmentation, and in leaf-texture, the supply departs on the marginal plan. *Ceterach officinarum*, DC., also supplies its pinnæ from the margin of its leaf-trace.

This division of a family between the one type and the other occurs also in the Pterideæ, where some genera show the marginal, some the extramarginal type. Two genera show some species following the marginal type and others following the extramarginal. *Trismeria trifoliata* (L.) Diels and *Adiantum sanctæ catherinæ*, hort., J. Sm., and *A. polyphyllum*, Willd., give off their pinna-traces in the normal extramarginal

manner. *Gymnogramma Pearcei*, *Ceropteris calomelanos*, and *C. calomelanos*, var. *chrysophylla*, show the marginal type in one of its varietal forms (cf. above, p. 352). The marginal type also occurs in *Pellæa hastata* (Thbg.) Prantl and *P. rotundifolia* (Forst.) Hk., *Cryptogramma crispa* (L.) R. Br., and in *Cheilanthes argentea* (Gmel.) Kze. and *C. myriophylla*, Desv., var. *elegans* (Pl. XXXV. fig. 21). In these Ferns the leaf-trace has a compact mass of tracheides, four-sided and wider on the adaxial than on the abaxial side of the petiole. The margin is simply nipped off to supply the pinnæ.

This form of leaf-trace appears also in *Notholæna affinis* (Mett.) Moore and *N. bonariensis* (Willd.) C. Chr., and the pinna-trace departs in the *Pellæa-Cheilanthes* fashion. But in *Notholæna sinuata* (Lag.) Klf. the leaf-trace is binary, the adaxial ends of each strand being distinctly hooked. Here the pinna-trace comes from the back of the hook and leaves a fairly long gap in the side of the leaf-trace strand after it has left it.

Two sharply contrasted types of pinna-supply are seen in *Pteris* and the genera associated with it. *Pteris cretica*, L., *P. biaurita*, L., and *P. umbrosa*, R. Br., have an ordinary marginal pinna-supply. But *Histiopteris incisa* (Pl. XXXIV. fig. 15 and Pl. XXXV. fig. 16) joins *Pteris* (*Litobrochia*) *macilenta*, A. Rich., and *Hypolepis tenuifolia* (Forst.) Bernh. in showing a combination of extramarginal and marginal types, the pinna-trace being built up of two parts, one coming extramarginally from the corner of the arch of the leaf-trace, the other marginally from its extremity.

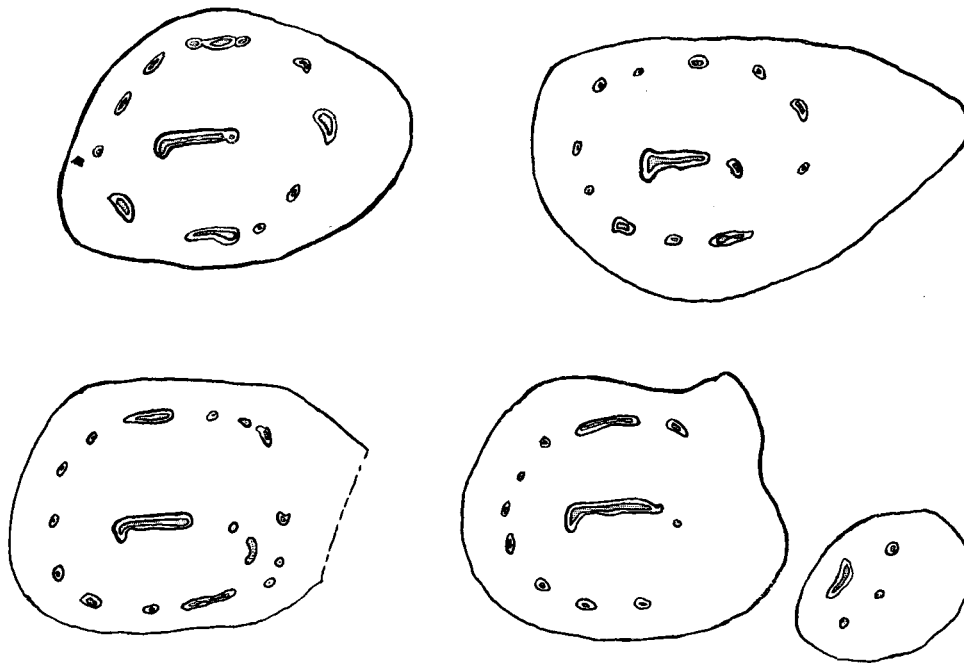
This can only be related to what appears in the Cyatheaceæ, in *Aspidium Moorei* and in *Leptochilus cuspidatus*. It bears no resemblance whatever to the process of pinna-supply in other species of *Pteris*.

In the Polypodiaceæ we have a consistent adherence to the marginal type of pinna-supply. *Polypodium aureum*, L., *P. vulgare*, L., *P. phymatodes*, L., *P. brasiliense*, Poir., *P. Schneideri*, hort., Veitch, and *Drynaria rigidula* (Sw.) Bedd. (Pl. XXXV. fig. 20), all have their pinna-traces simply nipped off from the edges of the leaf-trace bundles, and never give any suggestion of an extramarginal tendency.

Turning to the Eusporangiate Ferns, we find that the Marattiaceæ stand by themselves in their method of giving their pinnæ a vascular supply. In *Angiopteris erecta* (Forst.) Hoffm. and in *Marattia attenuata*, Lab., the pinnæ are supplied by several separate vascular strands. In the petiole there is a complete ring of vascular strands near the periphery, while the central portion is occupied, in *Angiopteris*,* by a single wide vascular strand, in *Marattia* by five or six strands in two groups, four or five strands making a curved set towards the abaxial face of the petiole, and one being situated below them towards the adaxial face. In both Ferns the pinnæ are supplied by the strands at the corner of the leaf-trace nearest to the pinna, by one or two strands from the abaxial and adaxial edges of the peripheral set, and by one strand cut off from the strand or strands in the central position (text-figs. 4 and 5).

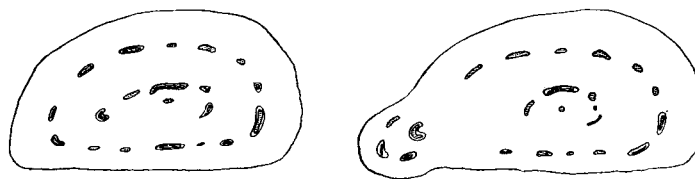
* In rather small leaves.

As the Marattian leaf-trace appears to be the horse-shoe type with much infolded margins, the pinnæ are supplied partly from the portions which correspond to the backs of the hooked portion of the horse-shoe type and partly from the infolded



TEXT-FIG. 4.—*Angiopteris evecta* (Forst.) Hoffm. Diagrammatic representation of the process of supplying the basal pinna with its vascular system.

margins, which are represented in the Marattian trace by the strands in the central position. A gap is left in the leaf-trace for some distance above the pinna. This is soon filled up by a movement into it of the leaf-trace strands at its edges and by new strands nipped off from these.



TEXT-FIG. 5.—*Marattia attenuata*, Lab. Diagrams illustrating the separation of the basal pinna-trace from the vascular strands of the petiole.

A similar process is seen in the petiole of *Helminthostachys zeylanica* (L.) Hk. There the pinna is supplied by strands which come partly from those forming the outer ring, and partly from the internal petiolar strand (*cf.* GWYNNE-VAUGHAN, '05, p. 266). This type of pinna-supply can hardly be called either marginal or extramarginal.

The case of *Helminthostachys* is not typical for the Ophioglossaceæ, however, for in *Botrychium lunaria* (L.) Sw. we do have a definitely marginal type of pinna-

supply (Pl. XXXV. fig. 17). The small plate of tracheides in the leaf-trace of this species extends towards the pinna and gives off its margin as the pinna-trace.

CHRYSLER has shown that this marginal type is not invariably found in the species of *Botrychium*. *Botrychium virginianum* nips off the edges of its leaf-trace prior to supplying its pinnæ, but these edges move along the inner faces of the leaf-trace strands and unite with them. The margins of the re-formed leaf-trace strands then pass off to the pinnæ.

These excursions outside of the Leptosporangiate Ferns help us but little in the interpretation of the great majority of forms of pinna-trace supply. The Marattian and Ophioglossean types of pinna-supply are apparently dependent on the special features of leaf-trace in these groups, and must be brought into line with the Filical types rather than employed as a means for their elucidation.

Two other regions of investigation may be entered before we attempt to make any general statements about the pinna-traces we have examined. There is first the supply to the terminal pinnæ. In general this has been found to be marginal. No matter what the outline of the leaf-trace in the lower part of the petiole, it generally becomes reduced to a simple narrow plate of tracheides with adaxial and abaxial strips of phloem lining it in the distal portion of the rachis. Often the supply is marginal to the pinnæ situated third or fourth in position below the tip of the leaf. In such pronouncedly extramarginal forms as *Histiopteris incisa*, *Pteris macilenta*, and *Hypolepis tenuifolia* the supply is marginal to the terminal pinnæ and to one or two below them. In *H. incisa* the supply is marginal to the pinna eighth in order from the tip of the leaf.

In the Cyatheaceæ we might expect a retention of a complicated outline for the leaf-trace up to near the tip of the leaf. In *Cibotium Schiedei* the strand is below the ultimate pinna an ellipse of tracheides, very "thin" on the adaxial side. The pinna is supplied by the departure of the lateral portion of this ellipse. Though the leaf-trace is a closed ellipse, the margins are, of course, on the adaxial side, and this supply is really of the extramarginal type. Exactly the same kind of trace appears below the ultimate pinna in the leaf of *Adiantum polyphyllum*, where the pinna is supplied after the same fashion.

In the early stages of the life of a Fern the method of pinna-supply is the marginal one. In the first pinnæ in a very early leaf of a plant of *Athyrium filix femina* the supply came from the edges of a simple plate of tracheides, in exactly the manner seen in most terminal pinnæ of mature leaves. In a later leaf the trace was binary and showed a tendency to form hooks at the edges of the two parts. Here the supply to the basal pinnæ was again marginal, though not from the extreme tip of the trace.

In a young plant of one of the Cyatheaceæ the supply was marginal in the first leaf, extramarginal in one considerably older (about the eighth).

In a relatively late leaf of a plant of *Peranema cyatheoides* (about the seventh

leaf) the supply to the basal pinnæ was marginal, of the type seen in the supply to the basal pinnæ in *Cystopteris montana*.

In a young plant of *Asplenium bulbiferum*, the supply to the basal pinnæ in the first leaf was marginal. The xylem formed a narrow plate, its long axis at right angles to the radius of the stem of the plant. From the margins of this line of tracheides the pinna-trace was simply nipped off.

In a young plant of *Asplenium lunulatum*, Sw., sub-sp. *erectum*, Bory, the supply to the basal pinnæ in a very early leaf was marginal. In the ninth or tenth leaf the supply was also marginal to the basal pinnæ. In the earlier leaf the group of tracheides was arranged in a compact mass, wide and slightly hollowed on the abaxial side and with two diverging extensions towards the adaxial corners. In the later leaf the abaxial portion had two little projections, each composed of only a few tracheides, while the adaxial extensions were much longer than in the earlier leaf. The axis is dictyostelic and the leaf-trace departs from the strands subtending the leaf-gap at a point where the two strands almost meet. The leaf-trace is single, though made up of two portions of xylem, coming each from one limb of the dictyostele. There is a common endodermis round the two portions of xylem and their surrounding phloem.

After the pinna-trace has left the petiolar bundle it develops differently in different Ferns.

Traces like that of *Loxosoma* are fully formed by the time they pass into the pinna.

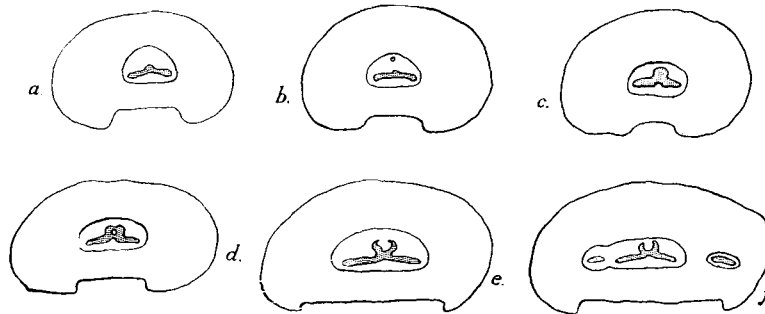
Gleichenia, *Osmunda*, *Todea*, *Hymenophyllum*, *Trichomanes*, *Balanium culcita*, *Dicksonia fibrosa*, *Histiopteris incisa*, *Hypolepis tenuifolia*, the Cyatheaceæ all have this type of pinna-trace.

Ferns with a "broken" leaf-trace (e.g. *Diacalpe aspidioides*) give off the pinna-trace as a "signet-ring," then break it into two in the pinna, and nip off the other strands from the aporachial ends of these two.

In *Davallia pallida* the pinna-trace passes into the stalk of the pinna as a dorsiventrally constricted mass of xylem enclosed in phloem (Pl. XXXIII. fig. 2). The xylem is wider in the centre of the pinna-trace than at the edges, where the margins are slightly curved towards the pro-rachial side of the stalk. A short distance out into the pinna-stalk there appear suddenly in the phloem on the aporachial side, first a single tracheide and then a small group, two or three in number (text-fig. 6, *b*). These are quite separate from the main set of tracheides of the pinna-trace, but as they increase in number the tracheides of the main trace extend towards them, and presently the two sets join (text-fig. 6, *c*). We have then a pinna-trace of triangular outline, the large amount of tracheides—and these greater in size of lumen than the others—in the central position, the margins being composed of a narrow set of small tracheides. Further out into the pinna the aporachial side of the group of tracheides becomes widened out on the peripheral face, so that there are two triangular groups attached to each other by the apices of the triangles (text-fig. 6, *d*). A little further

out still the aporachial set becomes broken up into two curved portions, and these separate from each other at their tips, so that the pinna-trace now has the outline of the leaf-trace (text-fig. 6, *e*). The supply to the pinnules goes off from this in just the way in which the pinna-supply leaves the leaf-trace (text-fig. 6, *f*). But in the pinnule there is no development of any accessory group of tracheides, and the pinnule-trace retains its narrow plate of tracheides throughout its length, giving off the supplies to the secondary pinnules from its margins.

In *Asplenium lucidum*, Forst., the supply to the pinna leaves the petiolar trace as a narrow strip of tracheides enclosed in phloem. Just as in *Davallia pallida*, a group of tracheides soon appears on the aporachial side of the pinna-stalk, becomes larger, and soon joins the main group of tracheides of the pinna-trace. The triangular set of tracheides thus formed soon splits at the apex of the triangle, and two portions, each like one part of the binary leaf-trace, remain attached to each other by their



TEXT-FIG. 6.—*Davallia pallida*, Mett. Series of diagrams to show the development of the pinna-trace.

middles. From this pinna-trace the supply to the pinnules is nipped off marginally. Just as in *Davallia pallida*, there is no appearance of tracheides in the pinnule-trace in the position of their occurrence in the pinna-trace.

In *Drynaria rigidula* the pinna-trace leaves the leaf-trace (Pl. XXXV. fig. 20) as a narrow plate of tissue, with about twelve tracheides. The tracheides in the centre of the plate are much larger than those at its edges, and as the strand passes out into the pinna these central tracheides rearrange themselves, crowding into a little four-sided group, the small tracheides remaining as narrow strips at the edges of the group. In this condition the vascular strand passes up to the tip of the pinna.

In *Asplenium præmorsum* the margin of the leaf-trace which goes off to the pinna remains as a narrow plate right through the pinna, only extending laterally and nipping off its edges when pinnules have to be supplied.

This survey of the pinna-trace and its development and elaboration in the Ferns confirms the impression given by an examination of the table on p. 354. There is a gradual rise of the extramarginal type out of the marginal, and then a lessening of this type until in the most advanced Ferns it disappears altogether and the marginal type remains. The comparison of the pinna-traces of the early leaves of various Ferns

shows that at first the marginal type prevails. And an examination of the ultimate branches of the Fern leaf reveals the marginal type in the great majority of species.

We have then to explain how this variation of type has come to be, and whether it can be related to any prominent features in the development of the vascular system in the Ferns. To what is the variation due? Can we trace it to the differences in the construction of the stele? Is it dependent on the length of the leaf, on the number of pinnæ, or on the state of division and subdivision of the pinnæ themselves? Or is the outline of the leaf-trace responsible for the differing points of departure of vascular supply for the appendages of the leaf?

SINNOTT has based his classification of leaf-traces upon the number of protoxylem groups present in them. On this basis he has separated Osmundaceæ from Marattiaceæ, and these from all remaining forms. The Osmundaceæ are protagonists of the extramarginal type of pinna-supply; the Marattiaceæ are divergent but consistent adherents of the same type; the real differences occur in "all remaining forms." The explanation of pinna-trace type cannot be in the number of protoxylem groups in the leaf-trace.

We are brought no nearer to an explanation by the work of PARMENTIER ('99),* whose classification of the Ferns of France on the structure particularly of their petioles is not too reliable. For his type-sections of these petioles have apparently been made at varying levels, and his arrangement depends much upon the comparison of sections taken at different distances from the base of the petiole. No attempt is made to compare one leaf-trace with another as they run from end to end of the leaf.

Two notable contributions to the knowledge of the evolution of the Filicinean leaf-trace are those of THOMÆ ('86) and BERTRAND and CORNAILLE ('02). In both of these papers a comprehensive survey of Fern-petioles is made and distinctive types are contrasted with one another.

From the leaf-traces of *Phegopteris*, *Onoclea*, *Aspidium*, THOMÆ makes an "*Aspidium*-type," which he joins with the "*Asplenium*-type" and the intermediate "*Struthiopteris germanica*-type" as a "*Polypodiaceous* type."

Against this he sets the "*Cyatheaceous* type." The transition from the one to the other is through *Hypolepis tenuifolia*,† *Pteris tremula*, and *Hypolepis repens*.

He makes the Marattiaceæ and *Cibotium* exceptional modifications of these types. He concludes that the different families of Ferns can be distinguished by the characters of the leaf-trace, but that a systematic arrangement of Ferns on anatomical grounds is quite outside of any serious consideration, and that only broad distinctions can be confirmed by the anatomy of the petiole.

The most interesting feature of his classes is the selection of the bridge from the *Cyatheaceous* type to the *Polypodiaceous* type. For we have seen that the pinna-

* Cf. PÉLOURDE ('06).

† In quoting the work of THOMÆ and BERTRAND and CORNAILLE I retain their nomenclature of the Ferns they describe.

trace of *Hypolepis tenuifolia* relates that of the Cyatheaceæ to that of certain species of *Pteris*. His contrast of an *Aspidium-Asplenium* type with that of the Cyatheaceæ finds an echo among the pinna-traces. So, too, does his opposition of the *Aspidium* leaf-trace to that of *Asplenium*.

A wider and more ambitious treatment of the leaf-trace is given by BERTRAND and CORNAILLE. No account of Fern-leaf anatomy can give other than a careful and grateful consideration of this exhaustive work. It abounds in curious details of minutest observation, many of them tucked away, unfortunately, in little corners where they easily lurk unnoticed. The Osmundean trace (that of *O. regalis*) is regarded as the prototype from which those of other Ferns are derived. The traces of *Todea barbara*, *T. Fraseri*, *T. superba*, *T. hymenophylloides*, *Aneimia collina*, *A. phyllitidis*, *Mohria caffrorum*, *Gleichenia dichotoma*, and *G. rupestris* are taken as variations of this Osmundean trace. The Cyathean trace of *Dicksonia antarctica* and *D. squarrosa* is the Osmundean trace with refolded adaxial arcs. Its variations occur in *Matonia pectinata*, *Dicksonia regalis*, *Cyathea medullaris*, *Alsophila australis*, and *Hemitelia Smithii*. Then comes the Onoclean trace of *Struthiopteris germanica*. A variant on it in *Onoclea sensibilis* prepares for *Polypodium phegopteris* and *Lomaria spicant*, while it appears, greatly reduced, in *Nephrodium molle* and *Doodia aspera*.

Within the wide range of variations of this type come the traces of *Davallia repens*, *Scolopendrium officinale* (the "polypodian hippocampus"), *Davallia fœniculacea*, *Asplenium ruta-muraria*, *A. trichomanes* (reduced in *Marsilia* and *Pilularia*), *A. Nidus-avis*, *Onychium japonicum*, *Davallia tenuifolia*, and *Pellea geraniifolia*. Amplified variations of the same type appear in *Gymnogramma tatarea*, *Blechnum brasiliense*, *Lithobrochia vespertilionis*, *Microlepia platyphylla*, *Polypodium Hera-cleum*, *Ceratopteris thalictroides*, *Goniopteris proliferum*, *Dennstaedtia davallioides*, and *Pteris aquilina*, while a very much reduced form appears in *Lygodium japonicum*, *L. scandens*, *Trichomanes radicans*, and *Hymenophyllum tunbridgense*. A Polybotryan trace, isolated in character, occurs in *Lomariopsis fraxinifolia*.

In contrast to these types is a Marattian trace of *Marattia fraxinea*, *M. Lancheana*, *Angiopteris evecta*, and *Kaulfussia æsculifolia*. The Ophioglossean trace of *Helminthostachys zeylanica*, *Botrychium rutaceum*, *B. virginicum*, and *Ophioglossum vulgatum* is derived from the Marattian trace.

Obvious situations for tourney-fields lie in the announcement of the Osmundean trace as the primitive type and in the assortment of heterogeneous leaf-traces under the Onoclean banner.

No early leaf I have examined shows a leaf-trace like that of *Osmunda regalis*; many show outlines not unlike that of *Aneimia collina* and *Lygodium scandens*. And a classification of *Doodia aspera* and *Blechnum brasiliense* alongside of *Asplenium ruta-muraria* and *Scolopendrium officinale*, with *Onoclea sensibilis*, *Polypodium phegopteris*, and *Microlepia platyphylla* not far off, gives no clue to the widely

divergent pinna-traces of these species. These Ferns may all rightly be of the Onoclean type, but that avails nought to explain why they supply their pinnæ in such very different ways.

But the leaf-trace headlines Osmundean, Cyathean, Onoclean, and Marattian stand clear and are suggestive. From the Osmundean and Onoclean groups there may be drawn types of leaf-trace which agree in supplying their branches on a definite plan which is seen in the earliest known Ferns, and which is found in those Fern-leaves which occur first in the development and in those parts of Fern-leaves which are regarded as primitive. And from the Onoclean group, too, can be taken other types which are now known to be high in the scale and which supply their pinnæ in a manner, so to speak, improved upon that dominant in the Osmundean and Onoclean groups. The marginal type of pinna-supply cuts up the Osmundean and Onoclean groups when it is applied as a differential factor. And the marginal type is at once the most primitive and the most advanced.

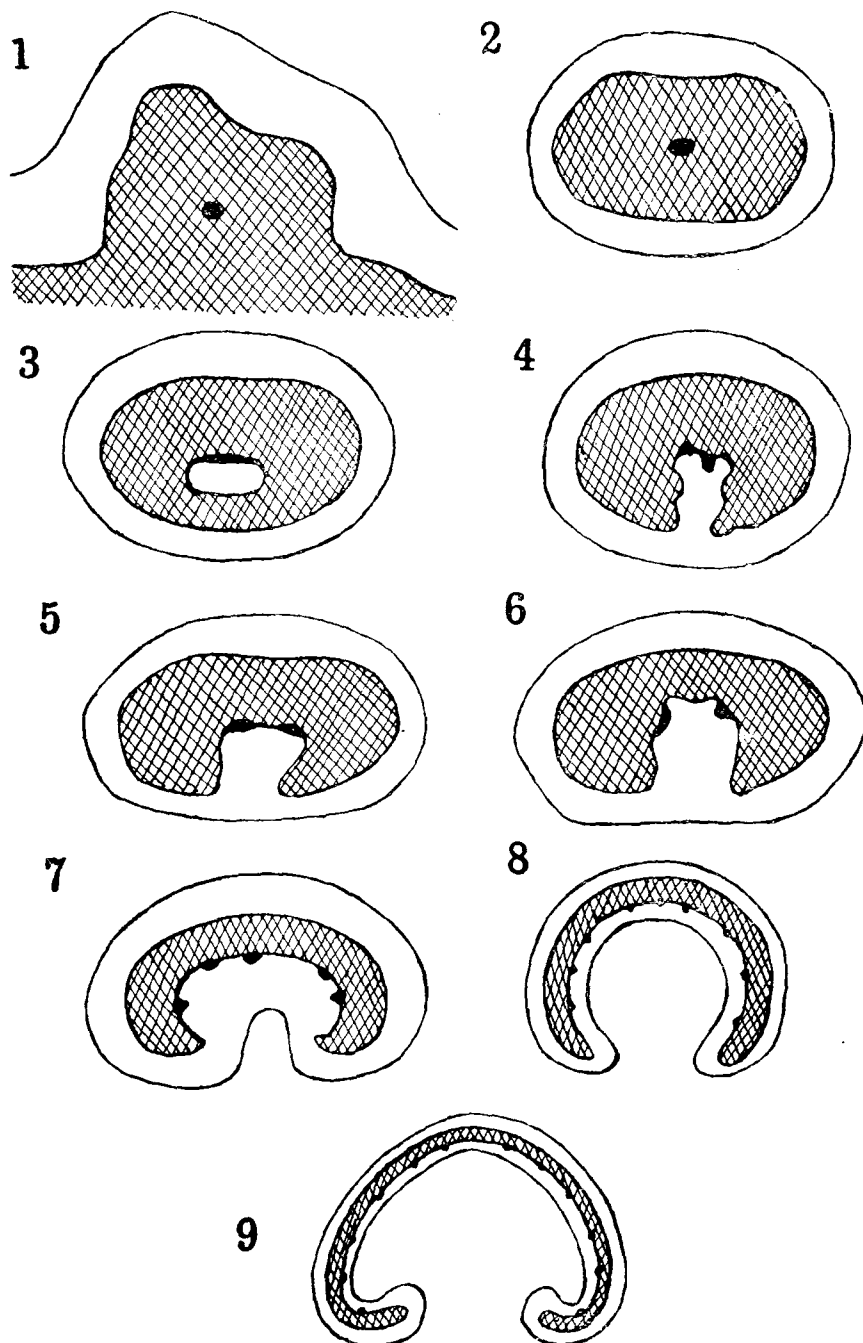
This presence of the marginal type at the bottom and at the top of the evolutionary ladder brings out prominently the need for discovering the factors that produced the intermediate extramarginal type. This is altogether dependent on the presence of the incurved hooks at the ends of the leaf-trace. It only appears where they are present, though sometimes hooks are present in leaf-traces that supply their pinnæ marginally. The evolution of the hooked leaf-trace must be the first factor in this development of the extramarginal type of pinna-trace.

This evolution is suggested by KIDSTON and GWYNNE-VAUGHAN ('08) in their description of the leaf-trace of *Thamnopteris Schlechtendalii*, Eichw. (text-fig. 7). There the leaf-trace arises as a swelling of the xylem of the stem. It passes off without leaving any gap or depression in the stem-xylem, then protoxylem appears almost centrally in it, an island of parenchyma occurs on the adaxial side of the protoxylem, this island increases in size, the protoxylem groups widen along the bay and the curved trace is produced, followed by a curving of the petiolar outline. These changes in the individual leaf-trace are held to indicate the changes undergone in the ontogeny and phylogeny of the adaxially curved leaf-trace so representative of the Filicales. The adaxial hooks thus remain as part of the adaxial side of an originally solid leaf-trace.

Such a solid leaf-trace does occur in several of the Zygopterideæ.

In *Dineuron ellipticum*, Kidston, and *D. pteroides*, Renault, the leaf-trace has an elliptical strand of xylem grooved at the ends. The pinna-traces depart from these ends as curved bars leaving no gaps in the tissues of the leaf-trace (text-fig. 8, *a*). In *Metaclepsydropsis duplex*, Williamson, the solid mass of tracheides in the leaf-trace has the outline of an hour-glass. The pinna-traces go off from the dilated ends of this leaf-trace (text-fig. 8, *c*). *Diplolabis Römeri* (Solms) supplies its pinnæ from the same relative position of the leaf-trace as do the two preceding species, but the arms of the leaf-trace are highly developed here in the normal petiole, though at its

base stages like the leaf-traces of *Dineuron* and *Metaclepsydropsis* have been found. *Etapteris diupsilon*, Williamson, has the ends of the arms very much developed,



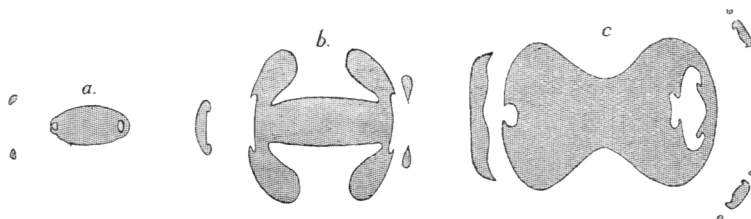
TEXT-FIG. 7.—Diagrams illustrating the departure of the leaf-trace in *Thamnopteris Schlechtendalii*, Eichw., sp. (After GWYNNE-VAUGHAN and KIDSTON.)

though the pinna-trace comes from the middle of the arm (*cf.* text-fig. 8, *b*), just from the position from which the pinna-trace goes off in *Dineuron*. Unfortunately

for the sake of minute comparisons with the living Ferns, these Zygoterideæ seem to have possessed four orthostichies of primary pinnæ. The pinna-traces which we have mentioned presently divide into two parts each, so that these Ferns must not be examined too critically for prototypes of leaf-trace. But there is at least a constancy in the position of origin of the pinna-trace-bars, as GORDON terms them. They come from the margins of the solid leaf-traces just from the points nearest to the appendages which it is their work to supply.

KIDSTON and GWYNNE-VAUGHAN have classified the Zygoterideæ according to the presence of a single row of appendages ("pinnæ") on each side of the main rachis or of two such rows.

Those genera already mentioned fall into their second class. The first class, with a single row of appendages on each side of the main rachis, includes *Ankyropteris bibractensis*, Renault, and *Clepsydropsis antiqua*, Unger. From the edge of the leaf-trace in *Clepsydropsis antiqua* the pinna-trace goes off as a closed ring. This



TEXT-FIG. 8.—Diagrams illustrating the pinna-trace departure in *a*, *Dineuron pteroides*, Renault; *b*, *Etapteris Scotti*, P. Bertrand; *c*, *Metaclepsydropsis duplex*, Williamson. (After P. BERTRAND, and GWYNNE-VAUGHAN and KIDSTON.)

type of pinna-trace occurs also in *Ankyropteris*. *Ankyropteris corrugata*, Williamson, has biserial primary pinnæ and one plane of symmetry. The leaf-trace has the outline of a double anchor—a modification of the *Etapteris-Diplolabis* type. The pinna-traces in this Fern leave the edges of the arms of the leaf-trace in very much the same way as those of *Diplolabis* leave its leaf-trace, but here there is only the one set of pinnæ to be supplied from each arm of the leaf-trace, and thus only one half of the leaf-trace arm is concerned in the process. It is just a *Diplolabis* type with half of the pinna-trace-bar suppressed. This *Ankyropteris*-type is another illustration of the effect of the position of the pinnæ relatively to the leaf-trace in affecting the point of departure of the pinna-trace. But the details of the departure of the pinna-trace in *Ankyropteris* recall the process in such an extramarginal type as *Didymochlæna truncatula*. The full growth of the pinna-trace has not been followed, but the sections of *Ankyropteris bibractensis*, var. *westphalensis*, P. Bertrand, which have been studied by PAUL BERTRAND (text-fig. 9) (*Études sur la fronde des Zygotéridées*, Lille, 1909), show the widening out of the tracheides at the part of the leaf-trace which is to supply the pinna, the appearance of a reparatory set ("anneau réparatrice interne") to ensure the continuity of the tissues of the arms of the leaf-trace past the point of pinna-trace departure, and the departure of the pinna-trace

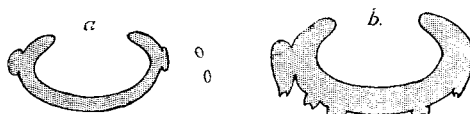
as a closed ring. In *Clepsydropsis* the actual margin of the leaf-trace goes off to supply a pinna; in *Ankyropteris* the pinna-trace leaves the leaf-trace in the extra-marginal way.

Where there are two orthostichies of primary pinnæ to be supplied from each arm of the leaf-trace, as there are in *Dineuron*, *Metaclepsydropsis*, *Diplolabis*, and *Etapteris*, the pinna-trace-bar leaves the leaf-trace on the side directed towards these pinnæ as a single curved mass of xylem, and then breaks into two parts, each of which moves



TEXT-FIG. 9.—Departure of pinna-trace in *Ankyropteris bibractensis*, var. *westphalensis*, P. Bertrand.
(After P. BERTRAND.)

out to a pinna. Where the pinnæ are uniseriate, as in *Ankyropteris*, the pinna-traces depart from the edges of the leaf-trace at the ends nearest to the pinnæ and move directly out to them. In *Tubicaulis solenites*, Cotta (text-fig. 10, *a*) (the C faces with its curve away from the axis—reverse of the living Fern), and in *Anachoropteris Decaisnei*, B. Renault (text-fig. 10, *b*), the pinna-traces leave the leaf-traces back from the edges, and the marginal set of tracheides is undisturbed throughout the rachis. But the pinna-trace in these two is a solid patch of xylem and not a closed ring. BERTRAND makes a suggestive explanation of the *Anachoropteris* type, deriv-



TEXT-FIG. 10.—Diagrams illustrating the departure of the pinna-trace in *a*, *Tubicaulis solenites*, Cotta;
b, *Anachoropteris Decaisnei*, Renault. (After P. BERTRAND.)

ing it from the type of *Dineuron pteroides* by development of the anterior hooks. He indicates how the position from which the pinna-trace departs in *Anachoropteris* corresponds with that from which the *Dineuron* pinna-trace goes off from the leaf-trace. This is an emphasis of the retention by the pinna-trace of the position of departure relatively to the leaf-trace. The pinna-traces of *Dineuron* and *Anachoropteris* correspond to the marginal and extramarginal types in the living Ferns, though we must remember that the *Dineuron* pinna-trace breaks into two parts after going off from the leaf-trace, and that it has to supply two orthostichies of pinnæ. This caution also applies to the pinna-trace of *Tubicaulis*, though the trace of *Anachoropteris* supplies but one pinna. Any discussion of the type of leaf in the Zygotpterideæ and Botryopterideæ as illustrated by these leaf-traces is out of place

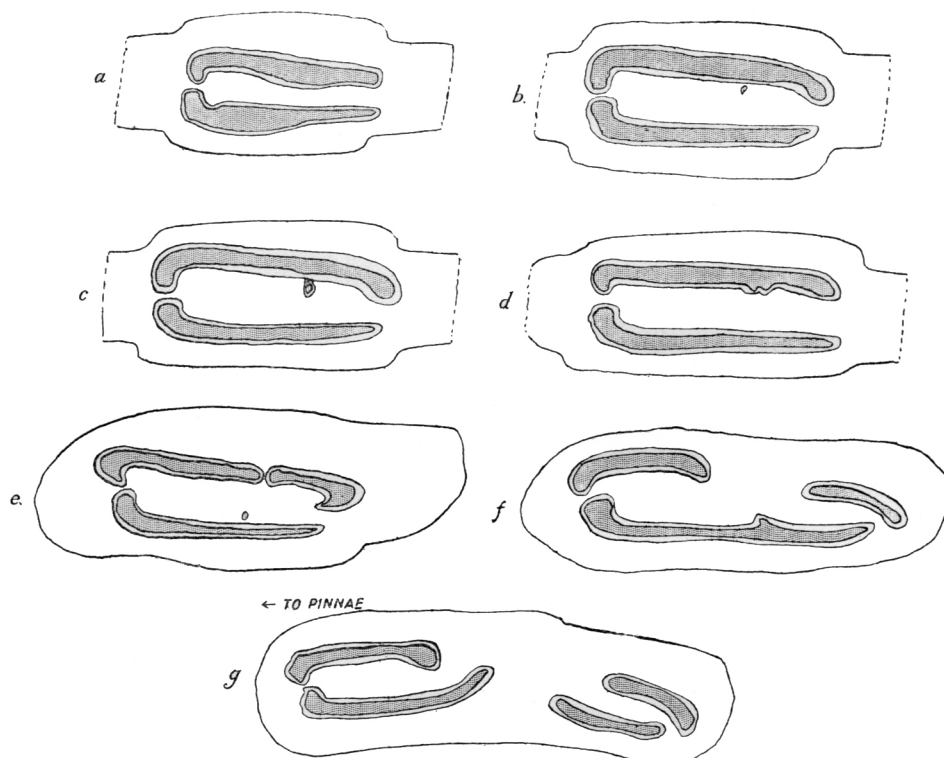
here. The useful information which these Ferns give us is that their pinna-traces departed from their leaf-traces at the points nearest to the pinnæ.

If we carry this into the living Ferns, any fundamental distinction between marginal and extramarginal types of pinna-trace breaks down—the pinna-traces go off just from the points which best serve the pinnæ. The distinction between the marginal and extramarginal types of pinna-trace must then be one due to the differences in leaf-traces, not in the pinnæ themselves. This is so far true. But a marked divergence from the type general within a family, such as that of *Balantium culcita* (pp. 350, 356) from the type of the Cyatheaceæ, must make us pause in the generalisation. We have in *B. culcita* a marginal type of pinna-supply, yet the general type in the Cyatheaceæ is a very elaborate extramarginal one. The changes in the leaf-trace of *Gleichenia flabellata* throw some light on the interpretation of this divergence. There the incurved margins of the leaf-trace round themselves off as circular groups of tracheides which run up along the face of the gaps caused by the departure of the pinna-traces (Pl. XXXIV. fig. 14), and then beyond the pinna-trace gaps unite to the remaining tracheides of the median part of the leaf-trace (text-fig. 3). The incurved edges of the leaf-trace in *Gleichenia* carry on the water-supply up the adaxial face of the leaf. The pinnæ are relatively large, and the pinna-traces make a considerable drain on the tracheides of the leaf-trace. Apparently such a drain would cause a serious deflection of water from the adaxial face of the petiole, and would probably cause a water-starvation of the successive sets of pinnæ above the basal pair. The incurved hooks of the *Gleichenia* leaf-trace have thus the task of carrying forward the water-supply from one pinna-gap to the next, and of providing sufficient water to counteract the drain of several sets of pinnæ.

We would thus expect to find a considerable development of incurved hooks in leaves possessing many pinnæ, and perhaps most distinctly in those leaves with many pinnæ arranged in close succession (*cf.* TANSLEY, *Ev. of Fil. Vasc. System*, p. 117, *cf.* p. 126). In the Cyatheaceæ the leaf generally possesses a long “tail” of lamina beyond the last pair of actual pinnæ. And in the Cyatheaceæ the leaf-trace beyond the last pair of pinnæ is an ellipse of tracheides, thin on the adaxial face (*cf.* p. 360). Just the same arrangement in the leaf-trace is found in *Adiantum polyphyllum*, where the leaf ends in a long “tail” similar to that of Cyatheaceous leaf. *Balantium culcita* has a much shorter leaf than the majority of the Cyatheaceæ; the pinnæ are relatively not heavy and are arranged at relatively considerable distances from one another. Almost the same remarks apply to the leaf of *Dicksonia fibrosa*, which has a marginal pinna-supply just like that of *Balantium culcita*. These are simple Cyatheaceæ (perhaps owing their simplicity to reduction) which have modified their type of vascular supply to the pinnæ in relation to their relatively short leaves. In the leaf of the majority of the Cyatheaceæ the complicated leaf-trace with its very much incurved margins is related to the large size of the leaf, the weight of the pinnæ, and their large number. The incurved edges of the leaf-trace persist beyond

even the last pair of pinnæ, in order to provide sufficient water-supply for the "tail" of the leaf.* The two exceptions, *Balantium culcita* and *Dicksonia fibrosa*, have relatively short leaves with pinnæ situated at greater distances from one another than are those of *Cyathea*, *Alsophila*, and *Hemitelia*. And these two have only slight hooks on the adaxial faces of their leaf-traces, a much simpler type of leaf-trace and marginal supply to the pinnæ.

An interesting confirmation of this view of the function of the incurved margins of the leaf-trace comes from *Botrychium virginianum* (CHRYSLER, '10). There the



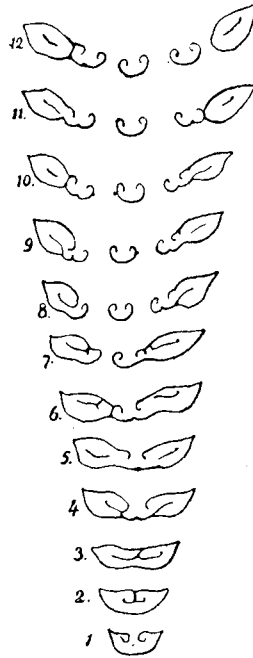
TEXT-FIG. 11. — *Botrychium daucifolium*, Wall. Diagrams illustrating the departure of the vascular supply to the first pair of sterile pinnæ.

margins of the leaf-trace strands nip off, pass along the adaxial face for a short distance, and then take up the position of margins for the leaf-trace when the pinna-trace goes off. This ensures a continuity of water-supply past the bases of the pinnæ. *Botrychium daucifolium*, Wall., affords us an example of a similar process (text-fig. 11). In the preparation for the departure of the vascular supply to the first sterile segments of the leaf there appears on the inner side of one of the two leaf-trace strands at first a single tracheide, then a small group of tracheides (text-fig. 11, *b*), which approaches the leaf-trace strand and finally unites with it (text-fig. 11, *c*). Part of the group then goes off with the portion of the leaf-trace strand

* See also *Diplazium marginatum*, where the supply is marginal to the nerve fourth in position from the tip of the leaf.

going to the pinna, the rest remains as the new margin of the leaf-trace strand (text-fig. 11, *d, e*). This process appears in the supply of the second pinna (text-fig. 11, *e, f, g*), but in relation to the other of the two leaf-trace strands.*

Still other examples illustrating the same process may be cited in *Matonia pectinata* (SEWARD, '99) and *Archangiopteris Henryi*, Christ et Gies. (GWYNNE-VAUGHAN, '05). In *Matonia* the incurved adaxial edges of the leaf-trace unite, their margins extend laterally and pass with the lateral portions of the leaf-trace into the pinnæ (text-fig. 12). The pinnæ are thus supplied with an internal system which probably meets the demand for a considerable water-supply without unduly



TEXT-FIG. 12.—Diagram illustrating the division of the single petiolar stele into the vascular strands of the pinnæ. (After SEWARD.)

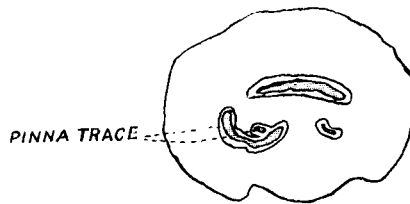
depleting the supply for the rest of the leaf. For the actual backs of the incurved hooks remain intact and pass up the rachis to carry water past the point of pinna-trace departure. This looks like a special case of the *Gleichenia*-type in which not only must water be carried up past the pinnæ for the needs of the higher parts of the leaf, but where the pinnæ must also be provided in quick succession with a good water-supply.

The pinna of *Archangiopteris Henryi* is supplied by strands which occupy much

* CHRYSLER argues from similar processes in *B. ternatum* that we have in this reinforcement a relic of an earlier system of passage of the margin along the face of the leaf-trace strand, such as we have already mentioned in *B. virginianum*. He sees no possible use for the reinforcing strand, as it is not connected at its base with the leaf-trace, and declares that it cannot convey water. But the structure of the tracheides in the Ferns is such that water might quite well be conveyed laterally from tracheide to tracheide even where the sets of tracheides are not continuous at their bases. Water can readily be deflected from the main strand into this reinforcing strand as soon as the two are in lateral contact, and thus the effect of the drain on the water-supply by the pinna-departure may be compensated for.

the same position in the rachis as do the parts of the leaf-trace which supply the pinna of *Matonia pectinata*. In *Archangiopteris*, however, the details are a little different, since the leaf-trace has a different outline from that of *Matonia*. One strand which goes into the pinna comes from the side of the curve of the leaf-trace set; the other comes from the abaxial face of the adaxial strand (text-fig. 13). The terminal part of the adaxial strand remains to carry the water past this pinna-gap. This terminal strand is itself reinforced below the departure-point of the pinnæ by internal accessory strands which come from the internal face of the abaxial curve.

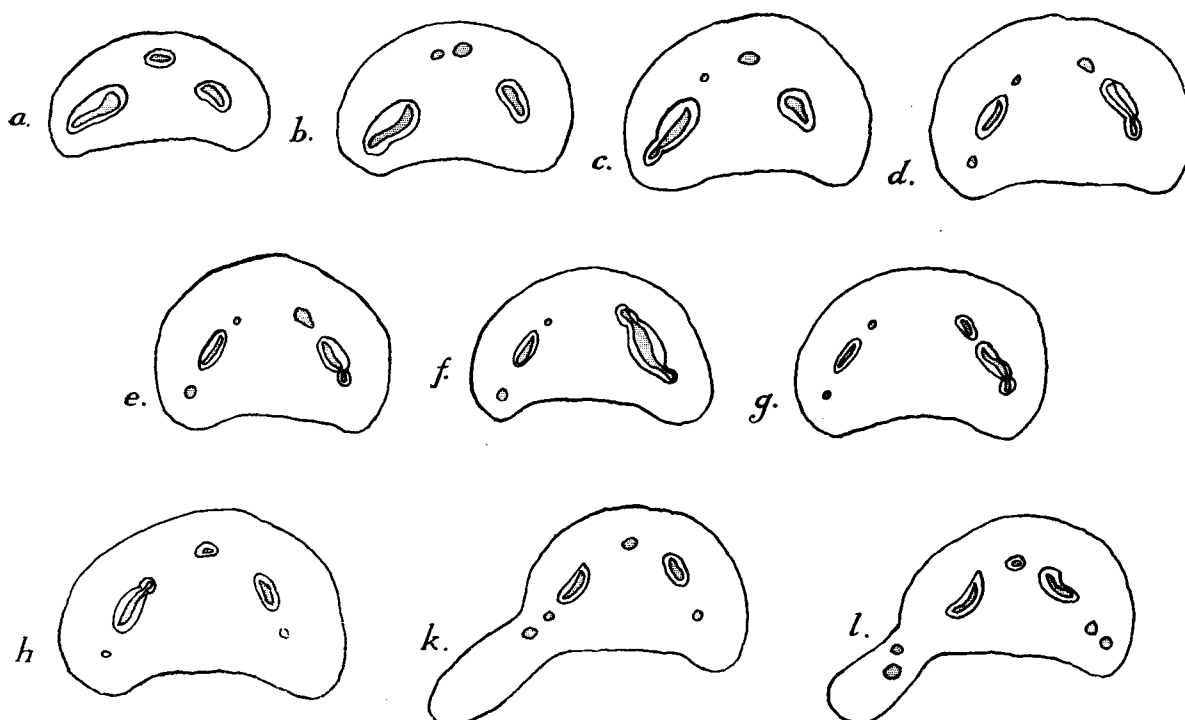
Wherever we find hooked adaxial portions in a leaf-trace, we do not find any evidence of a process of reinforcement, prior to the departure of the pinna-traces, of the parts of the leaf-trace supplying the pinnæ. But the incurved hooks do vary considerably in length and in their number of tracheides, according to whether the leaf is a long one or a short one, one with heavy pinnæ or one with light pinnæ, one with closely set pinnæ or one with pinnæ at considerable distances from one another.



TEXT-FIG. 13.—*Archangiopteris Henryi*, Christ et Gies. Diagram illustrating the method of departure of the pinna-trace. (After GWYNNE-VAUGHAN.)

An excellent example of the type of hook found in a long leaf with heavy pinnæ is that of *Didymochlæna truncatula* (Pl. XXXIII. fig. 7). Species of *Dryopteris* with shorter leaves and lighter pinnæ, like *D. filix mas*, have much smaller adaxial hooks. In *Microlepia hirta* and *M. platyphylla*, where the pinnæ are spread over approximately the same length of leaf, the adaxial hooks are of almost the same size; in *M. speluncæ*, whose leaves are usually larger, the adaxial hook is larger than in either of these. Leaves with relatively heavy pinnæ, like *Diplazium celtidifolium* or *D. marginatum*, have strongly developed adaxial hooks; those with fairly light pinnæ, like the *Blechnums*, have weak adaxial hooks. In all of these the adaxial hook appears to carry the water on from pinna-trace to pinna-trace along the leaf quite satisfactorily. Whenever the adaxial hook disappears and we get a marginal supply to the pinnæ, the system which carried forward the water disappears. On the whole, the appearance of the marginal type of pinna-supply seems to coincide with a reduction in the size or complexity of the leaf. This is by no means invariable, but a contrast of such outstanding genera as *Athyrium* and *Diplazium* (extramarginal) with *Asplenium* and *Ceterach* (marginal), or of *Hypolepis* and *Adiantum* (extramarginal) with *Pellæa*, *Cheilanthes*, and *Cryptogramma* (marginal), shows that there is some truth in the statement. A glance over the table on p. 354 confirms this

opinion that the extramarginal type of supply is found on the whole among large-leaved Ferns, the marginal type among the smaller-leaved genera. A few examples, like *Polypodium aureum* (marginal) and *Notholæna sinuata* (extramarginal), can be taken, which, if they stood alone, would prove the contrary proposition. The general survey tends to reveal the extramarginal type among large-leaved, heavily pinnate forms, the marginal type among the smaller-leaved, more lightly pinnate forms. *Davallia solida* gives us an interesting example of a process which may help the elucidation of the adoption of the marginal type of pinna-trace. The leaf-trace has



TEXT-FIG. 14.—*Davallia solida* (Forst.) Sw. Series of diagrams illustrating the changes in the leaf-trace during the period of supplying the lowest pair of pinnae.

two fairly large adaxial strands, with unincurved margins, and a small median strand (text-fig. 14, *a*). The adaxial strand gives off a portion marginally on the side directed towards the lowest pinna (text-fig. 14, *b* and *c*). This passes out into the base of the pinna; then another marginal portion is given off from the adaxial strand and follows the first strand into the pinna (text-fig. 14, *k*). The pinna-trace is binary and gives off two strands to the first pinnule. During the supply of the pinna by the leaf-trace the median strand nips off a small strand while one of the adaxial strands is preparing to give off its margin (text-fig. 14, *b*). This little strand passes to the adaxial strand and fuses with it between the giving-off of the first pinna-trace-strand and the second (text-fig. 14, *h*). The median strand itself moves towards the other adaxial strand and fuses with it just before it nips off the first strand for the pinna on that side (text-fig. 14, *e* and *f*). Some of its tracheides remain as the abaxial

portion of this adaxial strand; the rest simply separate away again and resume their position as the median strand (text-fig. 14, *g* and *h*). Thus both adaxial strands are reinforced by tracheides from the median strand during the period of pinna-trace departure. This process may well be compared with that which we have already considered in the supply of the pinnules by the pinna-traces of *Davallia pallida* and *Asplenium lucidum*, where the pinna-trace was reinforced by a set of tracheides appearing on the aporachial side before the pinnules were supplied. It is noticeable that, while the leaf-traces which supply their pinnæ on the marginal system are simpler in outline than those supplying their pinnæ extramarginally, there is a development usually of hooks on the *abaxial* ends of the leaf-trace strands (e.g. *Davallia*, Pl. XXXIII. fig. 2; *Gymnogramma Pearcei*, var. *robusta*, Pl. XXXIV. fig. 12). These probably serve the same purpose as the reinforcing strands of the leaf-trace of *Davallia solida*, or of the pinna-traces of *Davallia pallida* and *Asplenium lucidum*—they carry on the water-supply past the pinnæ, and prevent a too great reduction of the water-supply as we approach towards the tip of the leaf.

These explanations of the outlines of various leaf-traces are by no means provable in every leaf-trace which may be considered. But when they are taken in conjunction with one another and in relation to certain distinctive types of Fern-leaf they afford us the opportunity for a broad generalisation which finds confirmation in the arrangement of the species of Ferns in the table on p. 354.

But we have still to consider the possible advantage to be derived from the change from the extramarginal to the marginal type of pinna-supply. It seems to have occurred in a passage from a larger-leaved to a smaller-leaved form of the Fern (cf. above, p. 373). On that basis its occurrence is fairly easily to be explained. For in the small-leaved form the adaxial portion of the leaf-trace would be small and thin. To supply pinnæ from the back of a "thin" hook would be to give them a very exiguous pinna-trace. A *long strip* of tracheides can be more easily given off from an unincurved leaf-trace than from an incurved one. The width of the back of the hook is the dictator of the width of the pinna-trace in the extramarginal supply; the width of the marginal strip is the width of the whole margin of the unincurved leaf-trace. The back of a hooked leaf-trace is always "thin" as regards tracheides, and the pinna-traces which come off from it can give only a narrow strip of tracheides. Once the difficulty of carrying forward the water from pinna-departure to pinna-departure along the leaf was solved (by the development of hooks on the abaxial ends of the adaxial strands) the marginal type of supply must have been found an advantage rather than a drawback, because of its possibilities in supplying a long strip of tracheides to a departing pinna. This may explain its retention in the genus *Polypodium*, where the abaxial complications of the leaf-trace are often very elaborate and involved, and in some species of *Pteris* (*P. cretica*, *P. umbrosa*, etc.) where the abaxial arch and the lateral swellings of the leaf-trace are fairly prominent. The margins of the leaf-traces could be extended almost indefinitely to

supply the pinnæ, while the abaxial portion of the leaf-trace would carry forward the water-supply up the leaf. There is the possibility in the marginal type of "manufacturing" so much more tracheidal tissue than is really necessary for the pinna-supply that no contraction would take place between the pinnæ. But the actual *number* of tracheides does not seem to be altogether what keeps the water-supply in the proper direction. There is a *deflection* of the water-current towards the pinnæ. It is really largely this deflection which has to be counterbalanced by the provision of an accessory set of tracheides which will carry the water forward. Where the pinnæ are large the deflection will be great, and the counterbalancing hooks will be large; where the pinnæ are small the deflection is often negligible, and the hooks are small. This appears to lead to the conclusion that the Fern-leaf in phylogeny reduced its pinnæ, the hooks of the leaf-trace disappearing in relation to this. When a large leaf appeared later, an accessory tracheidal system developed in order to counterbalance the deflections which would have drained the upper part of the leaf of its legitimate water-supply.

All the features of the various leaf-traces cannot be fully explained on these theoretical grounds, but such distinctive characters of various leaf-traces as the incurved adaxial hooks connected with extramarginal supply to the pinnæ, the reinforcement of the adaxial strand in Ferns with marginal supply, and the retention of the marginal type even by fairly large-leaved species can certainly be interpreted if we consider broadly the needs of the pinnæ situated towards the tip of the leaf and the demand for water by large pinnæ of leaves possessing leaf-traces with unincurved adaxial edges.

A very interesting confirmation of the view that the adaxial or abaxial hooks of the adaxial portions of the leaf-trace serve to carry forward the water-supply past the pinna-departures is found in SALISBURY's paper on "The Determining Factors in Petiolar Structure." He calls attention to SINNOTT's conclusion (*Annals*, xxv. p. 187) that it is "extremely doubtful if the size of the transpiration current has had much influence on the development of the vascular supply," and confirms it for a species of *Polypodium*. There is a marked contraction of the xylem in a Fern-petiole, as SINNOTT reiterates (pp. 187, 188), as we approach near to its point of junction with the stem. SALISBURY, in emphasising the restriction of this contraction to a short distance at the base of the petiole, quotes (p. 266) the interesting observations of ORMSBY, which show that the effect of contraction in water mains is negligible where the length of contraction is small as compared with the total distance traversed. But there is a possibility of contraction of the water-supply to a great part of the leaf at other points than just at the base. The departure of every pinna might cause such a contraction in the supply for the rest of the leaf. Only in a leaf of considerable length with a single large pinna (if we can imagine such a leaf) would it be possible to neglect the effect of the departure of the pinna-trace upon the supply for the rest of the leaf. The confirmation of ORMSBY's rule is seen in the

elaborate precautions taken by leaf-traces to prevent undue contractions of their general water-supply due to the departures of successive pinnæ.

The two factors which have more than any others determined the development of the complications and simplifications of the margins of the Fern leaf-trace have been the need of carrying up past the earlier pinna-trace-departures a water-supply sufficient to meet the demands of the succeeding pinnæ and the terminal portion of the leaf. The need for supplying the separate pinna-traces has been met by the giving-off of the parts of the leaf-trace nearest to those pinnæ. As the leaves became larger and more heavily pinnate, provision was made for the water-supply of their increasing number by the development of the incurved hooks on the adaxial face of the leaf-trace. The departure of the pinna-traces took place still from the most conveniently situated part of the leaf-trace, but, as this was the back of a hook, the supply was extramarginal in origin. Then there seems to have been a condensation of the leaf-trace (perhaps in relation to a reduction in the size of the leaf), shown in the appearance of "broken" leaf-traces, either of the binary or of the many-stranded type. For some time the hooks were retained on the adaxial strands, but they gradually disappeared, and the pinna-supply was given off simply from the margins of the adaxial strands. Here and there arose again the need for carrying forward water past the pinna-trace departures. The marginal type of supply had become useful in its possibilities of extensive supply to the pinnæ. And the difficulty of carrying forward the water-supply to the ultimate parts of the leaf was solved by pressing the abaxial strand or the abaxial portions of the adaxial strands into the service. Sometimes the adaxial strands were reinforced from the median strand as necessity arose; at other times they were provided throughout their length with incurved abaxial hooks. If one may risk another generalisation from these details, it would seem that the Fern leaf in the course of its phylogeny had developed first in respect of *length*, at the same time as its appendages increased in size. Then there came a reduction both in the length of the leaf and in the size of the appendages, the reduction in length preceding the reduction in the size of the appendages. By that time the Fern leaf-trace had become thoroughly adapted to the needs of the leaf, and the later reductions or amplifications in special cases made but little change on the configuration of its adaxial portion, but mainly affected the abaxial part. Indeed, in the marginal type of pinna-supply which occurs in the more advanced Ferns we have the *most improved* type, and one which has proved to be the most adaptable.

In conclusion, I desire to express my thanks to Professor I. BAYLEY BALFOUR, F.R.S., for granting me the privilege of obtaining most of the material I have examined from the Royal Botanic Garden, Edinburgh, and for communicating this paper; to Professor F. O. BOWER, F.R.S., and Professor D. T. GWYNNE-VAUGHAN, F.L.S., for much helpful criticism; and to Dr W. T. GORDON, F.R.S.E., for assistance in the preparation of the microphotographs.

BIBLIOGRAPHY.

- BERTRAND, C. EG., et CORNAILLE, F. ('02), *Étude sur quelques caractéristiques de la structure des Filicinaées actuelles*.
- et P. BERTRAND ('11), *Le Tubicaulis Berthieri* (sp. nov.), C. Eg. Bertrand et P. Bertrand.
- BERTRAND, PAUL ('09), *Études sur la fronde des Zygoptéridées*, p. 127.
- ('11), *Nouvelles remarques sur la fronde des Zygoptéridées*.
- BOODLE, L. A. ('01), "On the Anatomy of the Gleicheniaceæ," *Annals of Botany*, xv. pp. 703-744.
- BOWER, F. O. ('12), "Studies in the Phylogeny of the Filicales: II. *Lophosoria*," *Annals of Botany*, xxvi. pp. 269-320.
- CHRYSLER, M. A. ('10), "The Nature of the Fertile Spike in the Ophioglossaceæ," *Annals of Botany*, xxiv. pp. 1-18.
- COMPTON, R. H. ('09), "The Anatomy of *Matonia sarmentosa*, Baker," *New Phytologist*, viii. pp. 299-309.
- DAVIE, R. C. ('12), "The Structure and Affinities of *Peranema* and *Diacalpe*," *Annals of Botany*, xxvi. pp. 245-266.
- ('13), "The Pinna-Trace in the Filicales," *Report, British Association Meeting, 1913*, p. 709.
- GORDON, W. T. ('11), "On the Structure and Affinities of *Diplolabis Römeri* (Solms)," *Trans. Roy. Soc. Edin.*, xlvii., pt. iv., pp. 711-736.
- ('11), "On the Structure and Affinities of *Metaclepsydropsis duplex* (Williamson)," *Trans. Roy. Soc. Edin.*, xlviii., pt. i., pp. 163-190.
- GWYNNE-VAUGHAN, D. T. ('01), "Observations on the Anatomy of Solenostelic Ferns: I. *Loxsonia*," *Annals of Botany*, xv. pp. 71-97.
- ('03), "Observations on the Anatomy of Solenostelic Ferns, Part II.," *Annals of Botany*, xvii. pp. 689-740.
- ('05), "On the Anatomy of *Archangiopteris Henryi* and other Marattiaceæ," *Annals of Botany*, xix. pp. 259-271.
- ('11), "Some Remarks on the Anatomy of the Osmundaceæ," *Annals of Botany*, xxv. p. 525.
- and KIDSTON, R. ('08), "On the Origin of the Adaxially-curved Leaf-trace in the Filicales," *Proc. Roy. Soc. Edin.*, xxviii. pp. 433-436.
- — "On the Fossil Osmundaceæ," *Trans. Roy. Soc. Edin.*, Part I., vol. xlv. pp. 759-780; Part II., vol. xlvi. pp. 213-232; Part III., vol. xlvi. pp. 651-667; Part IV., vol. xlvii. pp. 455-476.
- KIDSTON, R. ('08), "On a New Species of *Dineuron* and of *Botryopteris* from Pettycur, Fife," *Trans. Roy. Soc. Edin.*, vol. xlvi. pp. 361-364.
- PARMENTIER, P. ('99), "Recherches sur la structure de la feuille des Fougères et sur leur classification," *Ann. Sc. nat. Bot.*, 8^e sér., ix. pp. 289-361.
- PÉLOURDE, F. ('06), "Recherches anatomiques sur la classification des Fougères de France," *Annales des Sciences nat. Bot.*, 9^e sér., iv. pp. 281-372.
- SALISBURY, E. J. ('13), "The Determining Factors in Petiolar Structure," *New Phytologist*, xii. pp. 281-289.
- SEWARD, A. C. ('99), "On the Structure and Affinities of *Matonia pectinata*, R. Br.," *Phil. Trans. Roy. Soc.*, B, vol. 191, pp. 171-209.
- SINNOTT, E. W. ('10), "Foliar Gaps in the Osmundaceæ," *Annals of Botany*, xxiv. pp. 113-115.
- ('11), "The Evolution of the Filicinean Leaf-trace," *Annals of Botany*, xxv. p. 167.
- TANSLEY, A. G. ('08), *Lectures on the Evolution of the Filicinean Vascular System*.
- THOMÆ, K. ('86), "Die Blattstiele der Farne," *Jahrb. f. wiss. Bot.*, xvii. pp. 136, 140 et seqq.

EXPLANATION OF PLATES.

All the figures are from untouched microphotographs.

Plate XXXIII. figs. 1-8.

Fig. 1. Transverse section of the petiole of *Asplenium obtusatum*, Forst., showing the departure of the vascular supply to the two basal pinnae. $\times 38$.

Fig. 2. Transverse section of the petiole of *Davallia pallida*, Mett., showing one pinna-trace nipped off from the leaf-trace, and the other in process of development. $\times 42$.

Fig. 3. Transverse section of the petiole of *Aneimia hirta* (L.) Sw., showing the departure of traces to the basal pinnae. $\times 40$.

Fig. 4. Transverse section of the petiole of *Aneimia collina*, Raddi. $\times 20$.

Fig. 5. Transverse section of the petiole of *Loxsonoma Cunninghami*, R. Br., showing development of pinna-trace. $\times 30$.

Fig. 6. Transverse section of the petiole of *Loxsonoma Cunninghami*, showing departure of pinna-trace. $\times 30$.

Fig. 7. Transverse section through one of the adaxial bundles of the petiole of *Didymochlæna truncatula* (Sw.) J. Sm., showing the development of the "extramarginal" type of vascular supply to the basal pinna. $\times 55$.

Fig. 8. Transverse section of the petiole of *Leptopteris hymenophylloides*, A. Rich., showing the departure of one of the pinna-traces. $\times 44$.

Plate XXXIV. figs. 9-15.

Fig. 9. Transverse section of the petiole of *Odontosoria chinensis* (L.) J. Sm., var. *Veitchii*, below the basal pinnae, showing the development of the pinna-traces. $\times 44$.

Fig. 10. Transverse section of the petiole of *Hymenophyllum demissum* (Forst.) Sw., showing one pinna-trace separated from the leaf-trace, and another in process of separation. $\times 42$.

Fig. 11. Transverse section of the petiole of *Blechnum orientale*, L., showing the development of one of the basal pinna-traces. $\times 40$.

Fig. 12. Transverse section through one of the strands of the leaf-trace of *Gymnogramma Pearcei*, Moore, var. *robusta*, showing the pinna-trace in process of being given off. $\times 40$.

Fig. 13. Transverse section of the petiole of *Balantium culcita* (L'Hérit.) Klf., showing the extension and buckling of the ends of the leaf-trace prior to the departure of the pinna-trace. $\times 20$.

Fig. 14. Transverse section of the petiole of *Gleichenia flabellata*, R. Br., showing the formation of the isolated cylindrical strands before the pinna-traces depart. $\times 33$.

Fig. 15. Transverse section of the petiole of *Histiopteris incisa* (Thbg.) J. Sm., showing the development of two pinna-traces. $\times 30$.

Plate XXXV. figs. 16-23.

Fig. 16. Transverse section of the petiole of *Histiopteris incisa* (Thbg.) J. Sm., showing the completion of one of the pinna-traces. $\times 33$.

Fig. 17. Transverse section of the petiole of *Botrychium lunaria* (L.) Sw., showing the formation of one of the pinna-traces. $\times 33$.

Fig. 18. Transverse section of the petiole of *Odontosoria retusa* (Cav.) J. Sm., showing one pinna-trace free from the end of the leaf-trace, and the other in process of development. $\times 30$.

Fig. 19. Transverse section of the petiole of *Onoclea sensibilis*, L., showing the method of vascular supply to the basal pinnae. $\times 46$.

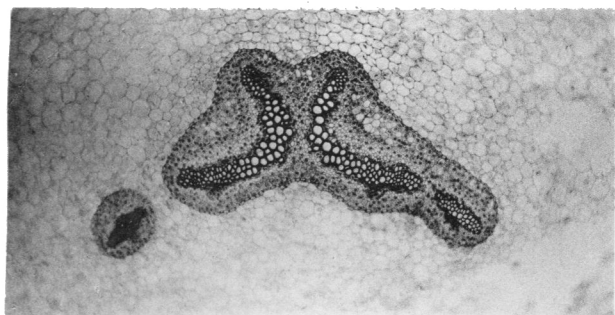
Fig. 20. Transverse section of one of the adaxial strands of the leaf-trace of *Drynaria rigidula* (Sw.) Bedd., showing the separation from it of a pinna-trace. $\times 53$.

Fig. 21. Transverse section of the petiole of *Cheilanthes myriophylla*, Desv., var. *elegans*, showing the method of separation of the basal pinna-traces. $\times 33$.

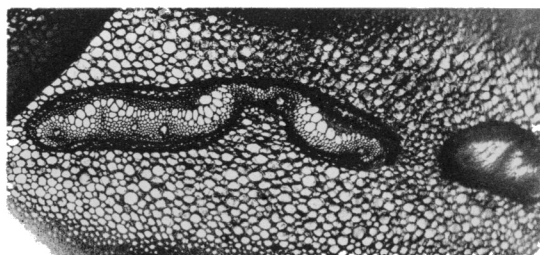
Fig. 22. Transverse section of the petiole of *Pteris cretica*, L., showing the extension of the ends of the leaf-trace, prior to the departure of the basal pinna-traces. $\times 33$.

Fig. 23. Transverse section of the rachis of the leaf of *Aneimia collina*, Raddi, showing the method of vascular supply to the last two pinnae. $\times 42$.

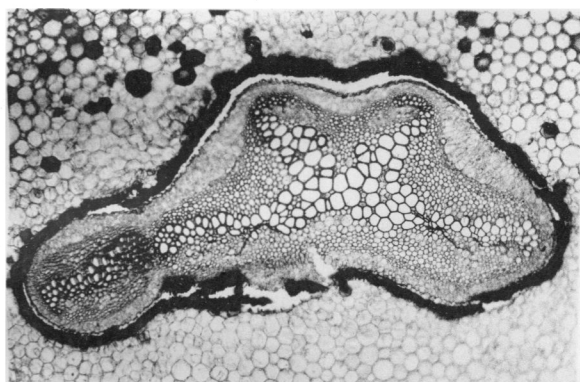
DAVIE : PINNA—TRACE IN FERNS.



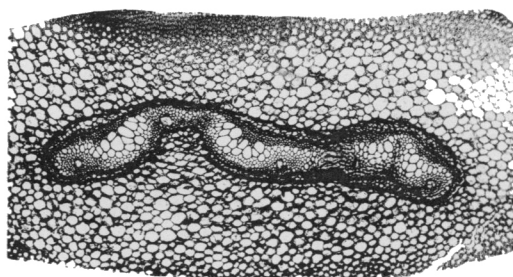
1



5



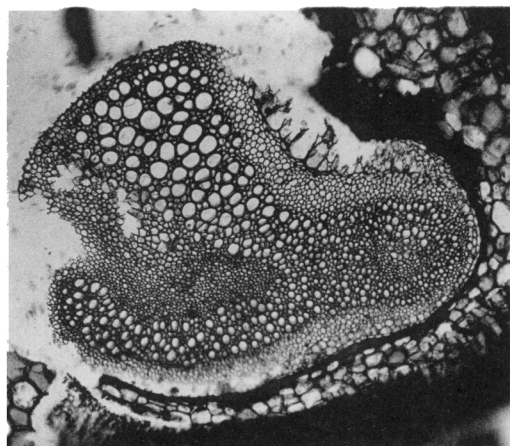
2



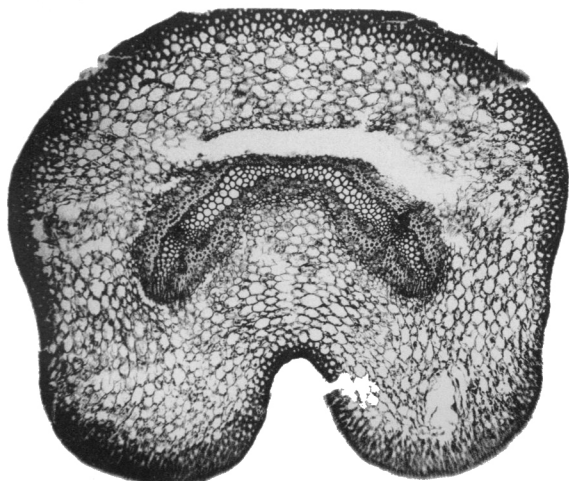
6



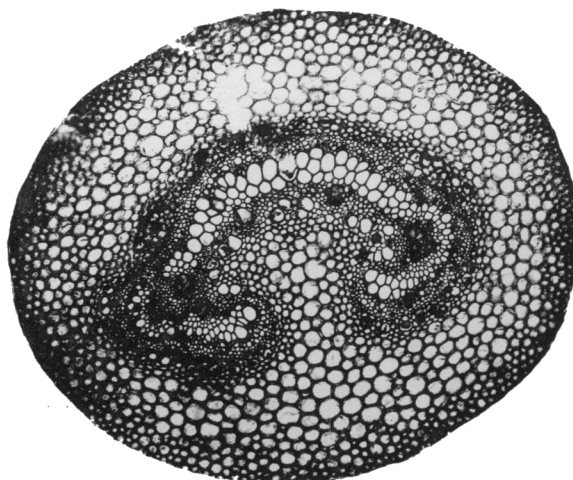
3



7

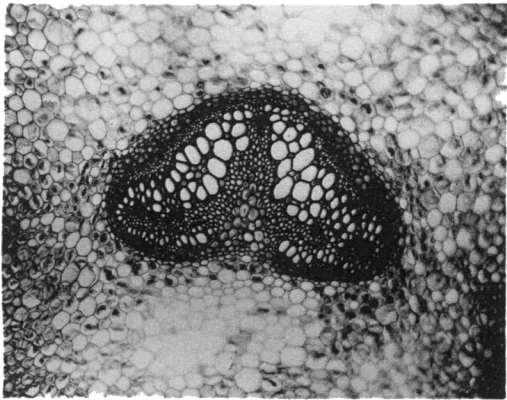


4

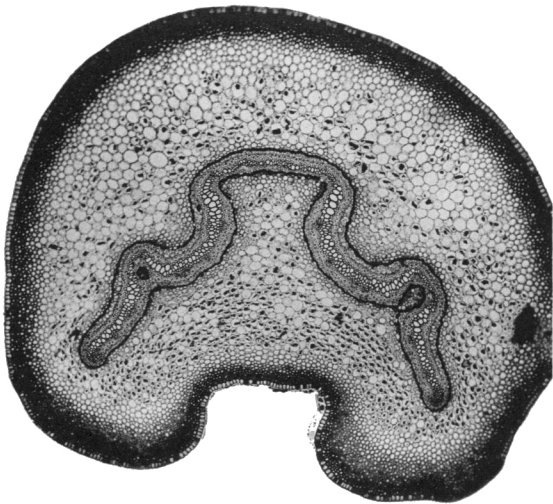


8

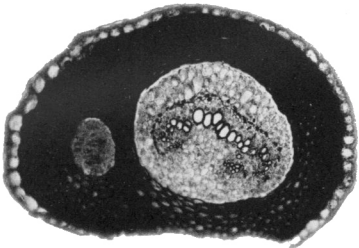
DAVIE : PINNA—TRACE IN FERNS.



9



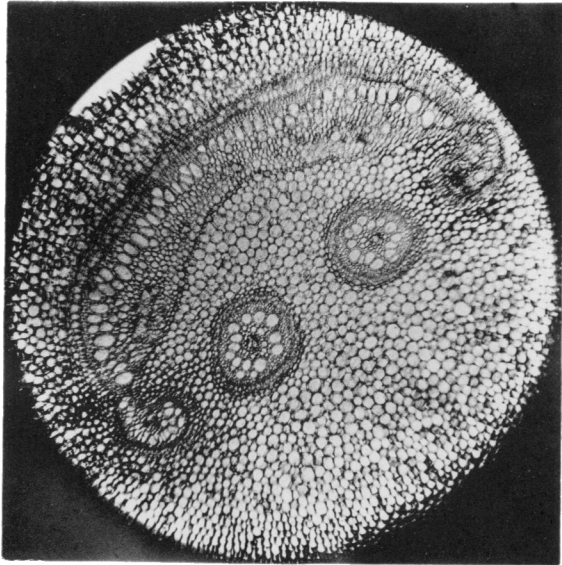
13



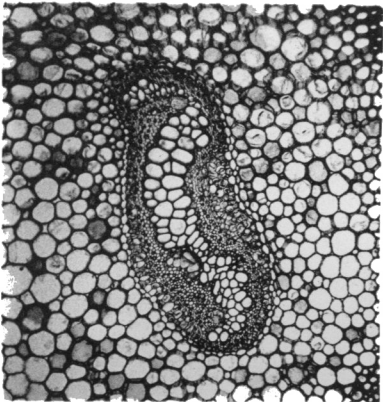
10



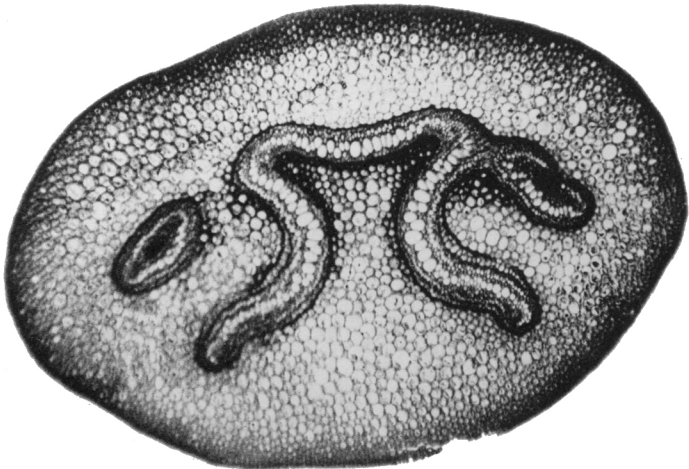
11



14

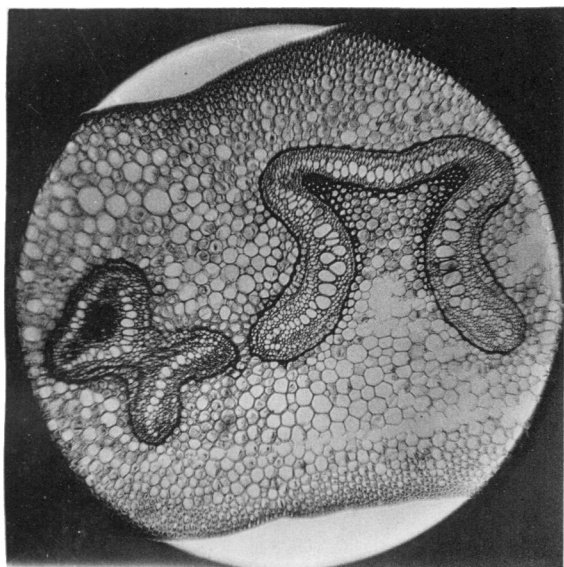


12

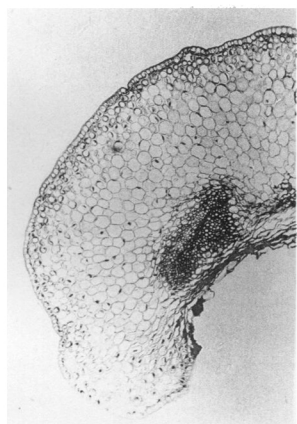


15

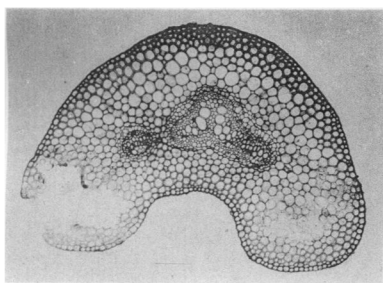
DAVIE : PINNA—TRACE IN FERNS.



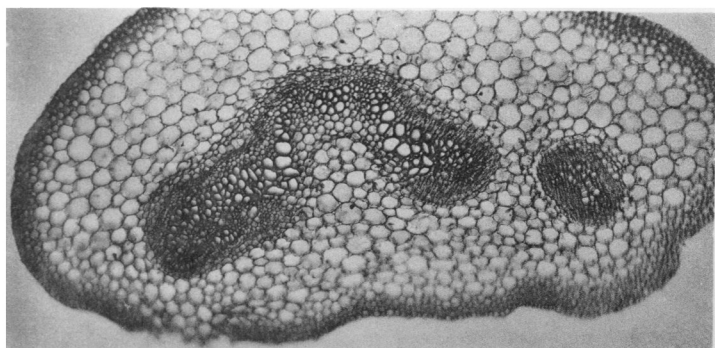
16



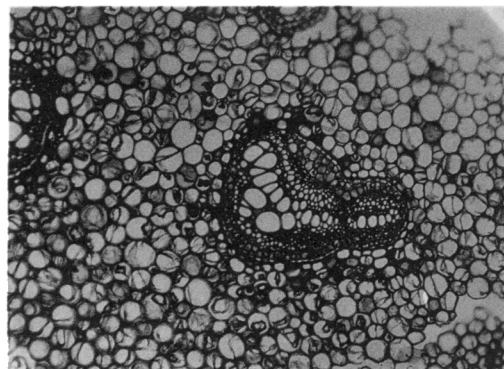
17



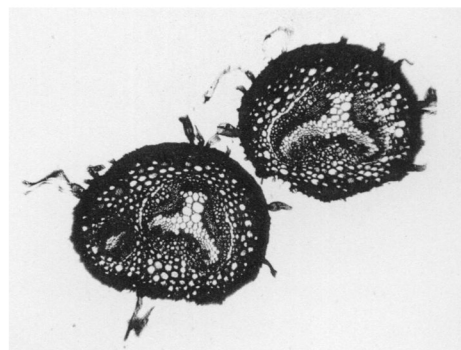
18



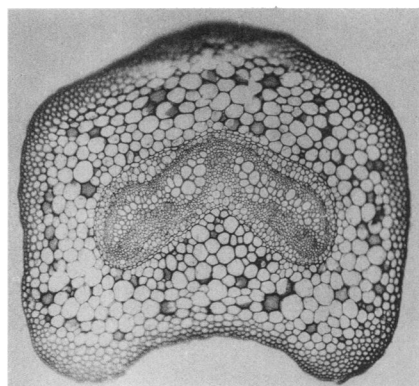
19



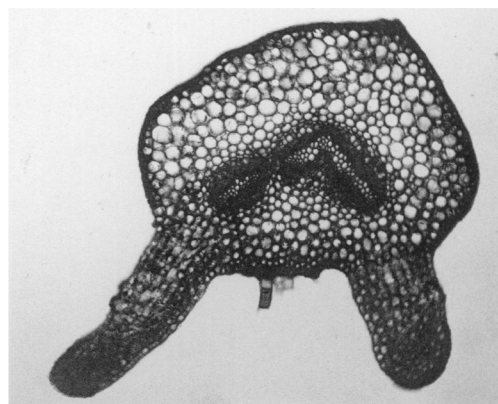
20



21



22



23