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# Studies in the Venation and Systematics of Polypodiaceae

II. Venation of Polypodiaceae (2) and of some other ferns

by

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# Introduction for part II

Polypodiaceae in the strict sense is a family of higher leptosporangiate ferns with about 1100 species in more than fifty genera. Generic delimitation within the family is currently based on such features as leaf architecture, venation pattern, trichomes, and soral construction, especially the soral commissure and receptacular paraphyses. However, these characters are still insufficiently known, being mostly based on outdated and/or fragmentary information.

In part I of this study, the venation of 23 genera of Polypodiaceae was described for adult leaves and/or ontogeny. In this second report, the venation is described for 25 additional genera of the family and also for some families other than Polypodiaceae for purposes of comparison. The characterization of the venation of Polypodiaceae will be mainly based on the ontogenetic evidence from this study, and the different features emphasized in this characterization will be utilized for the generic classification of Polypodiaceae in part III of this report.

# **Pyrrosia MIRBEL**

The venation of adult leaves of *Pyrrosia* was described by authors such as COPELAND (1947), HOLTTUM (1954) and NAVAR (1961a); that of the juvenile leaves of *P. lingua* (THUNB.) FARW. is as follows (Figs. 356-365): the first leaf is spathulate, with simple or few branched veinlets (356-358). After pseudo-monopodial mid-vein is formed (359-360), opposite acroscopic and basiscopic branches of the lateral veins anastomose with each other, forming areoles without included veinlets (361-362). In the succeeding leaves, excurrent included veinlets appear in the areoles except in costal ones which usually have no included veinlets (363-366). Recurrent veinlets appear in the later leaves (366).

A similar venation pattern is observed in *Pyrrosia* aff. varia (KAULF.) FARW. (Fig. 367). In this species, however, recurrent included veinlets are sometimes observed in the costal areoles.

In Pyrrosia adnascens (FORST.) CHING (Figs. 368-371), the outer rows of areoles have excurrent



Figs. 356-375. 356-366: Pyrrosia lingua, juvenile (356-365) and adult (366) leaves. 367: Pyrrosia aff. varia, part of adult leaf. 368-371: Pyrrosia adnascens, part of adult leaf (368-370) and showing outline of leaf. 372: Pyrrosia nummularifolia, adult leaf. 373-375: Pyrrosia linearifolia. 373: part of sterile adult leaf. 374-375: P. linearifolia var. heterolepis, sterile (374) and fertile (375).

included veinlets only (Figs. 368–370). In *P. nummularifolia* (Sw.) COPEL. (Fig. 372), excurrent included veinlets are usually simple. Similar to this is the venation of *P. linearifolia* (HOOK.) CHING (Fig. 373), though some excurrent veinlets are forked and/or united to each other in var. *heterolepis* TAGAWA (Figs. 374–375). The venation of *Saxiglossum taenioides* (C. CHR.) CHING is also similar to that of the above-stated species.

In Pyrrosia angustata (Sw.) CHING, included veinlets are more or less irregular in direction,



Figs. 376-399. 376-377: Pyrrosia shearerii, adult leaf. 378-380: Drymoglossum piloselloides, sterile (378-379) and fertile (380) leaves. 381: Drymoglossum fallax, sterile. 382-392: Microsorium (Phymatodes) fortunei, juvenile leaves. 393-399: Microsorium (Phymatodes) vieillardii, juvenile leaves.

as seen in P. lingua, but towards the apex of the leaf, they are usually excurrent.

In *Pyrrosia shearerii* (BAK.) CHING, there are more than ten rows of narrow areoles between costa and margin. Each major areole is oriented parallel to the rachis, and divided into several smaller areoles by connecting veinlets (377). The innermost areoles are very narrow, and often have recurrent veinlets. Lateral veins from the costa are thick and nearly straight. Included veinlets have irregular directions (376).

Among the species observed in this study (except those mentioned above), all the included

veinlets are excurrent in: P. hastata CHING, P. floccigera (BLUME) CHING, P. varia (KAULF.) FARW., P. polydactylis (BAK.) CHING, P. penangiana (HOOK.) HOLTT., P. nuda (GIES.) CHING, P. mollis (KUNZE) CHING and P. mannii (GIES.) CHING. Included veinlets are irregular in direction (as in P. shearerii) in: P. boothii (HOOK.) CHING, P. stigmosa (Sw.) CHING, P. subfurfuracea (HOOK.) C. CHR. and P. splendens (PRESL) CHING.

### **Drymoglossum PRESL**

The venation of the adult leaves of *Drymoglossum piloselloides* (L.) PRESL was described by HOLTTUM (1954) and NAYAR (1957); that of the juvenile leaves has not been studied. The venation of *D. piloselloides* is as follows (Figs. 378–380): in both round and elliptic sterile fronds, there are three to four rows of areoles on each side of the costa. The innermost rows of areoles are with simple or few branched recurrent included veinlets. Included veinlets are irregular in direction in the outer rows of areoles. Areoles in the marginal row are small, and have recurrent included veinlets only, if any. In the fertile fronds (380), marginal areolesare very small and much reduced, and are soriferous.

In the adult leaves of *Drymoglossum fallax* v.A.v.R. (Fig. 381), areoles are also in three to four rows on each side of the costa. The costal areoles have no included veinlets, or sometimes are open with an excurrent included veinlet in the larger areoles. The areoles of outer rows have excurrent free veinlets only, if any.

### **Microsorium LINK**

The venation of the adult leaves of *Microsorium* was examined by many authors, notably by HOLTTUM (1954), NAYAR (1961b, 1963b), TINDALE (1961) and MITSUTA (1981); that of the juvenile leaves was observed by GOEBEL (1918) for *M. pustulatum* (G. FORST.) COPEL., by NAYAR (1963b) for *M. pteropus* (BL.) COPEL. and *M. lucidum* (ROXB.) COPEL., and by MITSUTA (1981) for *M. punctatum* (L.) Fée, *M. (Phymatodes) vieillardii* (METT.) COPEL., *M. (Ph.) fortunei* (MOORE) CHING and *M. (Ph.) scolopendria* (BURM.) COPEL.

The venation of the juvenile leaves of different species of *Microsorium* is similar as also is that of *Lepisorus* spp. (Figs. 160–169, 170–184, 185–193). Juvenile leaves of *Microsorium* spp. have venation with a few rows of areoles on each side of the costa. Each areole has usually a recurrent included veinlet only (389–392, 399, 406–409), and excurrent included veinlets are only formed by irregular branches of recurrent included veinlets (392, 410). My observations on the juvenile leaves of *Microsorium* coincides with those of GOEBEL and NAYAR.

Only a small difference is observed between the venation of the adult leaves of *Microsorium* s.str. and *Phymatodes*. In *Microsorium punctatum* (Fig. 411), the large areoles are almost parallelogrammic in outline, and form several rows on each side of the costa. Similar large areoles are observed in *M. linguiforme* (METT.) COPEL. and *M. membranaceum* (DON) CHING. In *Phymatodes scolopendria* (BURM.) CHING, the large areoles are irregular in shape, and they are not arranged in definite rows (Fig. 412). Similar large areoles are observed in *Ph. fortunei* (MOORE) CHING with simple, narrowly oblong fronds. These differences are not apparent in the juvenile leaves Studies in the venation and systematics of Polypodiaceae



Figs. 400-416. 400-410: Microsorium (Phymatodes) scolopendria, juvenile leaves. 411: Microsorium punctatum, part of lamina of adult leaf. 412: Microsorium (Phymatodes) scolopendria, part of lamina of adult leaf. 413: Microsorium (Phymatodes) vieillardii, part of pinna of adult leaf. 414: Diblemma samarensis, part of adult leaf. 415-416: Leptochilus axillaris, part of adult leaf.

nor even in the adult leaves of more deeply dissected species as *Ph. vieillardii* (METT.) FOURN. (413).

In larger leaves of *Microsorium*, the costal areoles are very narrow, and usually lack included veinlets. *Microsorium cuspidatum* (DON) TAGAWA has pinnate fronds and approximately the

aspect of a *Polypodium*, but the venation is typical for *Microsorium*. The venation of *Phymatosorus* diversifolius (WILLD.) PIC. SER. (*Microsorium*, COPEL.) is similar to that of *M. vieillardii* (Fig. 413).

#### **Diblemma J. SMITH**

The venation of the adult leaves of *Diblemma* was described by COPELAND (1947). The material I observed (Fig. 414) well accords with his description.

Elongate coenosori are borne on the outer border of the outermost row of areoles, or occasionally sparsely scattered also on the inner veinlets. In the latter case, sori are small, round to oblong.

# Leptochilus KAULF.

The venation of the adult leaves of *Leptochilus axillaris* (CAV.) KAULF. was described and illustrated by HOLTTUM (1954) and NAYAR (1963a); that of the juvenile leaves of this species was also observed by NAYAR (l.c.) and reported as typical *Microsorium*-type.

The venation of the adult leaves of *Leptochilus axillaris* is rather characteristic (Figs. 415–416). Near the distal part of the frond, the venation is as found in *Microsorium* (415), but dawnwards pentagonal costal areoles are formed between the primary innermost areoles.

#### Paraleptochilus COPEL.

The venation of the adult leaves of *Paraleptochilus decurrens* (BL.) COPEL. was described by COPELAND (1947), HOLTTUM (1954), NAYAR (1963a) and others. According to their and also my observations, the venation of *Paraleptochilus* (Figs. 417–419) is similar to that of *Microsorium*.

# **Colysis PRESL**

The venation of the adult leaves of *Colysis* was described by COPELAND (1947), HOLTTUM (1954), EVANS and MICKEL (1969) and others, and is similar to that of *Microsorium* (Figs. 442–443).

In the juvenile leaves of *Colysis* (Figs. 420–441), reticulate venation is formed as in *Microsorium* with areoles at first having recurrent included veinlets only (427–429, 438–440).

# **Dendroglossa PRESL**

The venation of the adult leaves of *Dendroglossa* was described by COPELAND (1947), and by HOLTTUM (1954) for *D. minor* (FÉE) COPEL. My observation (Fig. 444) coincides with COPELAND's description. HOLTTUM compared the venation of this species to that of *Leptochilus axillaris*, which, however, is usually more complex (Figs. 415–416). The venation of *D. minutula* (FÉE) COPEL. is similar to that of *D. minor*. Studies in the venation and systematics of Polypodiaceae



Figs. 417-444. 417-419: Paraleptochilus decurrens, part of adult leaf. 420-429: Colysis hemionitidea, juvenile leaves. 430-441: Colysis pothifolia, juvenile leaves. 442-443: Colysis hemionitidea, part of adult leaf. 444: Dendroglossa minor, adult leaf.

# Drynariopsis (COPEL.) CHING

The venation of the adult leaves of *Drynariopsis heraclea* (KUNZE) CHING was described by COPELAND (1947), HOLTTUM (1954) and others; that of the juvenile leaves has not been observed.

In smaller lateral lobes of *Drynariopsis heraclea* (Fig. 445), the main veins are nearly straight, with up to ten rows of large areoles on each side of the costa. The costal areoles are extremely narrow, and rarely contain included veinlets. The large areoles in outer rows are nearly

rectangular, and parallel to each other. Each large areole is divided into many smaller areoles by connecting veinlets between the outer and inner borders of the areoles. These smaller areoles usually have one or two free veinlets oriented in various directions within them.

Near the base of the frond, secondary and tertiary veins are usually not straight, and the venation is thus more or less irregular.

Young fronds are densely hairly beneath with multicellular hairs having pointed apices.

COPELAND and HOLTTUM did not describe the narrow areoles along the costa. Except for this, my observations accord with theirs.

# Pseudodrynaria (C. CHR.) CHING

The venation of the adult leaves of *Pseudodrynaria coronans* (WALL. ex METT.) CHING was described by COPELAND (1947) and NAYAR (1954, 1961c), the latter with illustrations; my observations accord with theirs.

The venation of the juvenile leaves of *Pseudodrynaria* (Figs. 446–459) is at first simple, or few forked (446, 447). In the latter case, the frond margin is serrate, indented between the veins. A pseudo-monopodial mid-vein is soon established (448, 449, 451). Lateral veinlets fork, and the opposite acroscopic and basiscopic veinlets anastomose. Areoles are at first without included veinlets (452, 453); in later leaves areoles have excurrent or sometimes recurrent included veinlets, (454–457), though the difference between 'excurrent' and 'recurrent' is not meaningful here as the pattern of branching of the lateral veins is variable. In larger leaves (up to 8 cm long), three to four rows of areoles are formed on each side of the costa (458, 459). Included veinlets are oriented in various directions and fuse with each other, often forming smaller areoles with included veinlets. The leaf margin is notched.

# **Aglaomorpha SCHOTT**

The venation of the adult leaves of Aglaomorpha was described by COPELAND (1947), and is similar to that of *Pseudodrynaria*, except in the fertile segments. The venation of the juvenile leaves of Aglaomorpha meyeniana SCHOTT (Figs. 460–475) is similar to that of *Pseudodrynaria coronans* (Figs. 446–459) although the juvenile leaves of *A. meyeniana* bear multicellular glandular hairs. Similar hairs are observed in young fronds of *A. splendens* (J. SM. ex HOOK. & BAUER) COPEL. and *A. pilosa* (J. SM. ex KUNZE) COPEL.

### Holostachyum (COPEL.) CHING

The venation of the adult leaves of *Holostachyum buchananii* (COPEL.) CHING was described by COPELAND (1947) and is similar to that of *Pseudodrynaria coronans* according to his as well as to my own observations (Fig. 476). The costal areoles are narrow, but usually easily distinguished from the costa. The frond is densely covered with long, soft, multicellular hairs.

# Thayeria COPEL.

The venation of adult leaves of *Thayeria cornucopia* COPEL. is similar to that of *Aglaomorpha meyeniana*; that of the juvenile leaves has not been observed.



Figs. 445-477. 445: Drynariopsis heraclea, small lateral lobe. 446-459: Pseudodrynaria coronans, juvenile leaves. 460-475: Aglaomorpha meyeniana, juvenile leaves. 476: Holostachyum buchanani, small lateral lobe. 477: Photinopteris speciosa, part of pinna of adult leaf.

# Photinopteris J. SMITH

The venation of the adult leaves of *Photinopteris* was described by COPELAND (1947), HOLTTUM (1954) and others, and is unique among the Drynarioid ferns. The costal veins of



Figs. 478-523. 478-479: Photinopteris speciosa, juvenile leaves. 490-502: Drynaria quercifolia, juvenile leaves. 503-512: Drynaria propinqua, juvenile leaves. 513-523: Drynaria sparsisora, juvenile leaves.

lateral pinna are usually zig-zag, and large areoles of the outer rows are elongate hexagonal in outline. At the basiscopic base of each pinna, there is a small auricle called a nectary often having isolated veinlets.

The venation of the juvenile leaves of *Photinopteris speciosa* (BL.) FRESL (Figs. 478–489) is similar to that of *Pseudodrynaria coronans* (Figs. 446–459), and also to that of some species of *Drynaria* (490–502, 503–512, 513–523), though the leaves are broader and the margin is undulate to entire. The juvenile leaves are simple with distinct stipes, and the lamina is covered with long multicellular hairs.

# Drynaria (BORY) J. SMITH

The venation of the adult leaves of *Drynaria* was described by COPELAND (1947), HOLTTUM (1954), NAYAR (1961c) and others; that of the juvenile leaves was observed and illustrated by NAYAR (1965) though he gave no specific name for his materials. Both excurrent and recurrent included veinlets are observed in his figures. In the present study, the venation was studied for juvenile leaves of *D. quercifolia* (L.) J. SMITH, *D. propinqua* (WALL. ex METT.) J. SMITH, *D. sparsisora* (DESV.) MOORE and *D. rigidula* (SW.) BEDD.

In the juvenile leaves of *Drynaria quercifolia* (Figs. 490–502), a reticulate venation is formed in a way similar to that of *Pseudodrynaria coronans* (446–458) and *Aglaomorpha meyeniana* (460– 475). In larger leaves (500–502), the large areoles are divided into smaller areoles by connecting veins which are originate as do included veinlets. Various included veinlets are observed in these smaller areoles.

The venation of the juvenile leaves of Drynaria propingua (Figs. 503-512) and D. sparsisora (513-523) is similar to that of D. quercifolia.

In the juvenile leaves of *Drynaria rigidula* (Figs. 524–534), included veinlets are few (530– 532). As older fronds develop, lateral pinnae are added to the basal part of the simple frond (532). In later leaves, the terminal portion is occupied by the uppermost lateral pinna (533).

The venation types of the adult leaves of most species are similar to each other, and also to *Drynariopsis* and *Aglaomorpha*. In the following species the venation is simpler and areoles often lack included veinlets: *Drynaria rigidula*, *D. mollis* BEDD., and *D. bonii* CHRIST. In *D. parishii* (BEDD.) BEDD. and *D. fortunei* J. SMITH, included veinlets are mostly excurrent.

### Lecanopteris REINWARDT

The venation of the adult leaves of *Lecanopteris* was described by YAPP (1902), COPELAND (1947), HOLTTUM (1954) and others; that of sterile leaves is similar to that of *Microsorium* and *Lepisorus* according to their, as well as my own, observations.

The venation of the juvenile leaves of *Lecanopteris carnosa* (REINW.) BL. is as follows (Figs. 535–545): The first leaf is spathulate, with simple (535) or pseudo-monopodial veins (536), or occasionally forked (537). In succeeding leaves, the lateral veins fork at a wide angle (538), and opposite acroscopic and basiscopic branches of lateral veins anastomose with each other (539, 540). Areoles are at first without included veinlets, and later recurrent ones are formed (541, 542). In later leaves, additional rows of areoles are added in a similar way. Tips of recurrent included veinlets are simple or a few times hamate, and some of these veinlets run to the distal border of the areoles in inner rows, forming smaller areoles inside (544). Leaves are simple until this stage, or sometimes hastate (543, 545).

On the rhizome of juvenile plants there are glands or glandular hairs of various types and scales; the scales are similar to the glandular hairs at first, attached at the base, but later are inequilaterally peltate (548, 549). A few types of glands or glandular hairs are observed on the young fronds (550).



Figs. 524-550. 524-534: Drynaria rigidula, juvenile leaves (524-533) and venation of adult leaves (534). 535-550: Lecanopteris carnosa. 535-545: juvenile leaves. 546: juvenile plant. 547-549: various branched hairs and scales on rhizome. 550: various glandular hairs on leaf.

# **Crypsinus PRESL**

The venation of the adult leaves of *Crypsinus* was described by BEDDOME (1883), COPELAND (1947), HOLTTUM (1954) and others; that of the juvenile leaves is rather variable. In *Crypsinus* hastatus (THUNB.) COPEL. (Figs. 551–563), areoles are at first without included veinlets (557, 558); later they have either or both recurrent and excurrent included veinlets (559–563), and the recurrent ones dominate. In the juvenile and semi-adult leaves of *C. enervis* (CAV.) COPEL. (Figs. 566–568), excurrent included veinlets are dominant in the outer rows of areoles, where

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Figs. 551-576. 551-565: Crypsinus hastatus. 551-562: juvenile leaves. 563-565: small fertile leaves. 566-568: Crypsinus enervis, juvenile (566) and semi-adult leaves (567-568). 569-571: Crypsinus taeniatus var. palmatus, semi-adult (569-570) and part of adult pinna (571). 572: Crypsinus pyrolifolius, small adult leaf. 573-574: Crypsinus taeniatus var. taeniatus, part of adult pinna. 575: Crypsinus taeniatus var. borneensis, part of pinna. 576: Crypsinus ebenipes, part of adult pinna.

they often anastomose with each other forming smaller areoles within the primary ones, or are united to the recurrent included veinlets. In *C. taeniatus* (Sw.) COPEL. var. *palmatus* (BL.) C. CHR. (Figs. 569, 570), both recurrent and excurrent included veinlets occur with a similar frequency outside the costal areoles, though the recurrent ones are dominant in the outermost

row of areoles.

In the adult leaves of *Crypsinus*, included veinlets are variable in most species (Figs. 564– 565, 571–575, 582). In *C. albido-squamatus* (BL.) COPEL. (Figs. 577–581), the outer rows of areoles have excurrent included veinlets only, each tip of which is simple or forked at an acute angle (577). At pinna apices, costal areoles are narrow and lack included veinlets, and the outer rows of areoles have either excurrent included veinlets only or none (578, 579). Sori are borne on the distal line of the loop of excurrent included veinlets (580), or in the narrower pinnae, on the outer margin of the costal areoles. In the latter case, areoles lack any included veinlets (581).

# Pycnoloma C. CHR.

The venation of the adult leaves of *Pycnoloma* was described by CHRISTENSEN (1929) and HOLTTUM (1954). The latter pointed out that the venation of *Pycnoloma* agrees with that of *Crypsinus*.

In the adult leaves of *Pycnoloma* (Figs. 583–585), there are three to four rows of areoles on each side of the costa. The costal areoles usually lack included veinlets, or sometimes excurrent included veinlets occur in the largest areoles. In the outer rows of areoles, excurrent included veinlets are dominant. The leaf margins are notched (585).

The veins of the strongly contracted fertile leaves of the three species are very different, with usually only costal areoles without included veinlets on each side of the costa.

The venation of the juvenile leaves has not been observed.

# Grammatopteridium v.A.v.R.

The venation of the adult leaves of *Grammatopteridium* was described by VON ALDERWERELT VON ROSENBURGH (1922) and COPELAND (1947).

The venation of *Grammatopteridium costulatum* (CESATI) C. CHR. (Figs. 586, 587) is similar to that of *Grypsinus* in the common occurrence of recurrent included veinlets. My own observations coincide with that of VON ALDERWERELT VON ROSENBURGH and COPELAND.

The venation of the fertile pinnae is much simpler than that of the sterile ones.

# **Holcosorus MOORE**

The venation of *Holcosorus* is very simple, as usually only costal areoles without included veinlets are on each side of the costa (Figs. 588–589). The leaf-margin is usually without notching, but a vestigial notch sometimes occurs near the leaf apex (589).

# Selliguea BORY

The venation of *Selliguea* was described by COPELAND (1947), HOLLTUM (1954) and others. The venation of the adult leaves of *Selliguea* is similar to that of *Crypsinus* according to those authors' as well as to my own observations (Figs. 598–600, 601–602). Both recurrent and

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Figs. 577-604. 577-581: Crypsinus albido-squamatus, various venation of broader (577-579), moderate (580) and smaller (581) pinnae. 582: Crypsinus trilobus, part of lamina. 583-584: Pyenoloma metacoelum, small leaves. 585: Pyenoloma murudense, adult leaf. 586-587: Grammatopteridium costulatum, part of adult leaf. 588-589: Holcosorus bisulcatus, part of fertile leaf. 590-597: Selliguea heterocarpa, juvenile to semi-adult leaves. 598-599: Selliguea feei, part of fertile leaf. 600-604: Selliguea lima, part of adult leaf (600-602) and variable venation of semi-adult leaves (603-604).

excurrent included veinlets occur in the outer rows of areoles. The costal areoles usually have one or two recurrent included veinlets.

In the juvenile leaves of *Selliguea heterocarpa* BL., areoles are small, and excurrent included veinlets are pre-dominant (590–591). In the semi-adult leaves of *S. lima* (v.A.v.R.) HOLTT. (Figs. 603–604), excurrent included veinlets are pre-dominant and often reach the distal border of the areoles. In an extreme case, lattice-like areoles are formed (604).

# Arthromeris (MOORE) J. SMITH

The venation of the adult leaves of *Arthromeris* was described by COPELAND (1947), DEVOL and Kuo (1975) and others. According to their observations as well as to my own, the venation



Figs. 605-625. 605-606: Arthromeris wallichiana, part of adult pinna. 607: Arthromeris lehmanii, part of adult pinna. 608: Polypodiopteris proavita, part of fertile pinna with undulate margin. 609-616: Loxogramme salicifolia, juvenile leaves. 617-619: Loxogramme duclouxii, juvenile leaves. 620-622: Loxogramme grammitoides, juvenile (620-621) and fertile (622) leaves. 623-625: Loxogramme conferta, semi-adult (623-624) and adult (625) leaves, all sterile.

of Arthromeris (Figs. 605–607) is similar to that of Crypsinus. The costal areoles are with recurrent included veinlets, and the outer rows of areoles contain both recurrent and excurrent veinlets, which are often united to each other, leaving various free veinlets within the smaller areoles. Excurrent included veinlets are pre-dominant in A. lehmanii (METT.) CHING (607). The margins of the pinnae are entire or slightly notched. The venation of the juvenile leaves has not been observed.

# **Polypodiopteris REED**

The venation of *Polypodiopteris* was described by COPELAND (1947); my own observations accord with his. In a few specimens, more than two rows of areoles on each side of the costa were frequent (Fig. 608). Sori are borne terminally on the tips of excurrent included veinlets or dorsal on the veinlets of the outer rows of areoles. In the latter case, the outer rows of areoles are divided into smaller ones.

# Loxogramme (BLUME) PRESL

The venation of the adult leaves of *Loxogramme* has been described by various authors, such as COPELAND (1947), HOLTTUM (1954), NAYAR (1955), DEVOL and KUO (1975), KONTA (1978) and others; the juvenile leaves were studied by NAYAR (1968) for *L. involuta* (BL.) PRESL and KONTA (1978) for *L. salicifolia* (MAKINO) MAKINO.

In the juvenile leaves of *Loxogramme* (Figs. 609-619, 620-621, 623-624, 626), the veins are free in the youngest stages (609-611), and later they anastomose. In some areoles, included veinlets are observed, mostly recurrent in *L. salicifolia* (609-616), but excurrent in *L. duclouxii* (617-619).

The venation of the adult leaves of *Loxogramme* is variable. In smaller or narrow leaved species, the venation is usually simple, the areoles without included veinlets (Figs. 622, 625, 627–629, 633). In species with medium to large leaves, the lateral veins are more or less robust and the areoles often have various types of included veinlets (Figs. 630–632). The tips of veinlets are not swollen.

### Anarthropteris COPEL.

The venation of the adult leaves of *Anarthropteris* was described by COPELAND (1947). The material I observed accords with his description. There are narrow costal areoles and smaller areoles in the outer rows. All areoles usually lack included venilets (Fig. 635).

### **Pleurosoriopsis FOMIN**

*Pleurosoriopsis* is sometimes regarded as a member of the Polypodiaceae (NAVAR 1977, etc.), especially by the character of branched glandular hairs of the gametophyte.

The veins of *Pleurosoriopsis* are free, and every veinlet enters a lobe of a pinna. The frond is anadromous in construction; tips of veinlets are swollen (Fig. 636).

It is also desirable to consider the venation of the ferns of some genera outside the Polypodiaceae for purposes of evaluation of the character and for comparison.



Figs. 626-644. 626-629: Loxogramme lankokiensis, adult leaves, sterile (626-628 left) and fertile (628 right and 629). 630-631: Loxogramme salicifolia, part of adult leaf. 632: Loxogramme nidiformis, part of adult leaf. 633-634: Loxogramme subselliguea, adult leaves, sterile (633) and fertile (634). 635: Anarthropteris lanceolata, fertile leaf. 636: Pleurosoriopsis makinoi, adult leaf. 637: Ctenopteris tenuisecta, lateral pinna. 638-639: Ctenopteris brevivenosa, lateral pinnae, sterile (638) and fertile (639). 640: Glyphotaenium sponginosum, part of leaf. 641-644: Ctenopteris sp. part of lateral pinna.

#### Venation of some families other than Polypodiaceae

# Grammitidaceae (Figs. 637–644)

Almost all the members of this family have free venation (637–639). In a few cases the veins are reticulate, as seen in *Glyphotaenium* (640) and some species of *Ctenopteris* (641–644). In these two genera, the basal acroscopic veinlets are included, as seen in *Polypodium*, although sori are usually borne dorsally on the veinlet.

# Gleicheniaceae (Figs. 645-646)

Veins are all free in this family except for occasional irregular anastomosis. The sori are dorsal or occasionally terminal on the basal acroscopic veinlets. The tips of veinlets are not swollen.

# Matoniaceae (Figs. 647-650)

The venation of Matoniaceae has been described by various authors: SEWARD (1899), TANSLEY and LULHAM (1905), COMPTON (1909), COPELAND (1947), HOLTTUM (1954) and others. The venation of the juvenile leaves of *Matonia pectinata* R. Br. was reported on by BOWER (1923, 1928).

Along the costa of *Matonia pectinata* are very narrow areoles, which seem to have not been given attention by the previous authors (647).

The venation of *Phanerosorus sarmentosus* (BAK.) COPEL. is often reported as free (COPELAND, 1.c.), but sometimes anastomoses are observed between the basal acroscopic and basiscopic branches, especially in fertile lobes (648–650).

# Dipteridaceae (Figs. 651-653)

The venation of the adult leaves of *Dipteris* was described by BOWER (1923, 1928), COPELAND (1947), HOLTTUM (1954) and others; that of the juvenile leaves by BOWER (1.c.) and WAGNER (1952) for *D. conjugata* REINW.

The venation is very complex in *Dipteris novoguineensis* POSTHUMUS. In this species, free included veinlets occur in the very small areoles, which are of the fourth or fifth order of division of the primary areoles (652). The venation is much simpler in narrower segments of *D. lobbiana* (HOOK.) MOORE (653).

### Cheiropleuridaceae (Figs. 654–664)

The venation of *Cheiropleuria* was described by various authors, for adult leaves by BOWER (1923, 1928), COPELAND (1947), HOLTTUM (1954), TAGAWA (1959) etc., and for juvenile leaves by BOWER (1.c.) and STOKEY and ATKINSON (1954). From my observations, the venation of the juvenile leaves of *Cheiropleuria bicuspis* (BL.) PRESL is as follows: The veins are simple to a few times branched pseudo-monopodially in the first and/or second leaves (654, 655), or somewhat dichotomous (656) as reported by STOKEY and ATKINSON (1.c.). The veins are still free



Figs. 645-673. 645: Dicranopteris curranii, part of fertile lobe. 646: Gleichenia japonica, part of fertile lobe. 647: Matonia pectinata, part of fertile pinna. 648-650: Phanerosorus sarmentosus, leaflets, sterile (648) and fertile (649-650). 650 was diagrammatically shown. 651-652: Dipteris novoguineensis, dichotomous main-vein (651) and large areoles enlarged (652). 653: Dipteris lobbiana, part of leaflet. 654-664: Cheiropleuria bicuspis, juvenile leaves. 665-673: Tectaria simonsii, juvenile leaves.

in the succeeding leaves (657–659), and anastomose sparsely in later stages (660–662). In these, only recurrent included veinlets are observed in the areoles and a costa is present. In later leaves, recurrent included veinlets elongate and fork, some of their branches arriving at the border of the areoles, forming irregular included veinlets inside the smaller areoles (663–664). The outermost areoles have only recurrent included veinlets. The costa produces alternate branches and, the tips of the veinlets swell evidently. The venation at this stage accords well with BOWER's observations (1.c.).



Figs. 674-710. 674-682: Tectaria decurrens, juvenile leaves. 683-692: Hemigramma decurrens, juvenile (683-689) and part of semi-adult leaf (690-692). 693-702: Quercifilix zeilanica, juvenile (693-700) and semi-adult (701-702) leaves. 703-710: Pleocnemia irregularis, juvenile leaves.

# Dryopteridaceae subfam. Tectarioideae (Figs. 665-749)

The venation of Tectarioideae was described by various authors, as COPELAND (1947), HOLTTUM (1954), DEVOL and KUO (1975) and others; that of the juvenile leaves was observed



Figs. 711-742. 711-720: Tectaria gemmifera, juvenile leaves. 721-728: Tectaria pseudo-sinuata, juvenile leaves. 729-735: Ctenitis eatonii, juvenile leaves. 736-742: Ctenitis subglandulosa, juvenile leaves.

by IWATSUKI (1968) for Tectaria.

In this study, observations were made of the juvenile leaves of *Tectaria simonsii* (BEDD.) CHING (pinnate to sub-bipinnate. Figs. 665–673) *T. decurrens* (PRESL) COPEL. (simple to pinnatified, 674–682), *T. gemmifera* (FÉE) ALSTON (sub-bipinnate, 711–720), *T. pseudo-sinuata* BROWNLIE (sub-tripinnate, 721–728), *Hemigramma decurrens* (HOOK.) COPEL. (simple to pinnatifid, 683–692), *Quercifilix zeilanica* (HOUTT.) COPEL. (simple to pinnate, 693–702), *Pleocnemia irregularis* (PRESL) HOLTT. (sub-bipinnate to tripinnate, 703–710), *Ctenitis maximowicziana* (MIQ.)





CHING Tripinnate to quadripinnate), *C. eatonii* (BAK.) CHING (bipinnate to tripinnate, 729–735), *C. subglandulosa* (HANCE) CHING (quadripinnate, 736–742), and *Lastreopsis sp.* (quadripinnate, 743–749).

In Tectaria simonsii (665–673) and Quercifilix zeilanica (693–702), the veins begin to anastomose at about the fourth to fifth leaf. Areoles are at first without included veinlets (669, 670), and later with either recurrent or excurrent ones, though recurrent ones predominate. In both of these species, rows of areoles along the costa are formed in the early juvenile leaves, but outer rows of areoles are not regular.

In Tectaria decurrens (674-682) and Hemigramma decurrens (683-692), anastomosis of veins occurs in a way similar to that of the two preceding species, but outer rows of areoles are usually formed in the early juvenile leaves (680-682, 689-692). The development of anastomoses seen in these two species is similar to that of such Polypodiaceous genera as Microsorium and Colysis.

In Pleocnemia irregularis (703-710) and Tectaria gemmifera (711-720), a single row of areoles without included veinlets is formed along the rachis and costae (709, 710). The fronds become more or less deeply dissected in these species. The venation of juvenile leaves of T. gemmifera as observed in this study is in accordance with the observations of IWATSUKI (1.c.).

The venation of juvenile leaves of *Ctenitis eatonii* (729-735) and *C. subglandulosa* (736-742) is similar to that of *T. gemmifera*, although anastomosis of veins occurs in later (6th to 7th, at the earliest) juvenile leaves in *T. gemmifera*.

In the species with quadripinnate fronds as *Ctenitis maximowicziana* and *Lastreopsis sp.* (unnamed species, see JONES and CLEMESHA 1976) (743-749), the veins are all free and the fronds are deeply dissected even in juvenile stages. In the latter species, a single veinlet enters each lobe.

#### Characterization of the venation types observed in Polypodiaceae

The behavior of the basal acroscopic branch of lateral veins seems to be an important character in the Polypodiaceae. It develops into an included veinlet in *Polypodium*, *Campyloneurum* and some other genera, or forms areoles without included veinlets along the rachis and/or costa in *Pleopeltis* (Fig. 153, etc.), *Phlebodium* (Fig. 276, etc.) and others. On the other hand, it may anastomose with the basal basiscopic veinlet from the adjacent vein and produce only recurrent included veinlets (especially in the juvenile leaves) in *Microsorium*, *Lepisorus*, *Lemmaphyllum*, etc.

In some taxa, areoles lack included veinlets. Among these, some are considered to be derived by simplification or reduction of the venation judging from the size of the plants or thickness of the leaves.

Observations on the ontogenetic development of the venation made here suggest important differences among such taxa and/or genera as the Microsorioid and Drynarioid ferns, *Pleopeltis* (s.str.) and *Lepisorus, Colysis* and *Loxogramme*.

The characterization of the types of venation of Polypodiaceae based on ontogenetic evidence, and a comparison with those of SADEBECK (1899), LUERSSEN (1889) and others, is still difficult, as the development of the venation of such peculiar taxa as *Pessopteris* (type of Venatio Anaxetii), *Niphidium* and *Christiopteris* has not been described. The following is a tentative classification based on my studies mainly of developmental patterns of the venation. Among these patterns, some seem to be further distinguishable by such character as non-swelling of the vein tips as in *Loxogramme, Anarthropteris*, etc. These differences and other characters will be made use of in the comments on the generic classification of the Polypodiaceae in the succeeding chapter.

# I. Free venation.

Ia. A single veinlet entering each solitary lobe.

Polypodium spp. (P. lindenianum, Figs. 87–88; P. friedrichsthalianum; P. fallax, 76–82; etc.) cf. Pleurosoriopsis makinoi (636); Grammitidaceae, spp. (Ctenopteris tenuisecta, 637; etc.)

- Ib. More than one veinlets entering each lobe, or leaves not deeply dissected. Polypodium spp. (P. vulgare, 26-32, 83; P. plumula, 33-43; P. fucoides, 99-101; etc.) Thylacopteris (T. papillosa, 120; etc.)
  - cf. Grammitidaceae p.p. (Ctenopteris brevivenosa, 638-639; etc.) Gleicheniaceae (Dicranopteris curranii, 645; Gleichenia japonica, 646; etc.)
  - Matoniaceae, part. (Phanerosorus sarmentosus, sterile, 648).

II. Reticulate venation: areoles totally lacking included veinlets.

Dictymia (D. mackeei, 126-129; etc.).

Eschatogramme (Dicranoglossum) (E. desvauxii, 293-294; etc.)

Holcosorus bisulcatus (588–589, see also VII)

- Polypodiopteris proavita (608, see also IVc, VII)
- Loxogramme spp. (L. grammitoides, casually, 620–622; L. conferta, 623, 625; L. lankokiensis, 626–629, see also VII; L. subselliguea, 633–634; etc.).

Anarthropteris lanceolata (casually, 635).

III. Reticulate venation: free included veinlets excurrent and single at all stages of frond development.

- Polypodium p.p. major. (P. chnoodes, 63-65; P. glaucophyllum, 86, 72-75; P. formosanum, 56, 84; P. fraxiniifolium, 114-115; P. caceresii, 116-117; P. myriolepis (included veinlet sometimes forked), 90; P. munchii (Microgramma munchii, included veinlet often forked and looped), 92-93; P. ensiforme (same), 94; etc.
- Schellolepis p.p. major. (S. arguta, 109-110; S. subauriculata; etc.)
- Synammia (130, included veinlet sometimes forked)
- Microgramma spp. (M. piloselloides, included veinlet sometimes forked, 224, 238-239; M. vacciniifolium, 232-234, 241; etc.)

Phlebodium aureum (occasionally, 276, 280, 286)

- cf. Grammitidaceae p.p. (Ctenopteris sp. 643-644; Glyphotaenium sponginosum, casually, 640)
- IV. Reticulate venation: included veinlet excurrent only in juvenile leaves, and plural in outer (beyond costal) areoles.
  - IVa. Included veinlet free.
    - Polypodium p.p. minor (P. cyathoides, irregular form, 119)
    - Campyloneurum spp. (C. phyllitidis, 250–251; etc.)
    - Pyrrosia spp. (P. adnascens, casually, see also IVb., 368-369; P. nummularifolia, see also IVc. 372; P. linearifolia, 373-375; etc.)
    - Drymoglossum fallax (see also IVb, IVc. 381)
  - IVb. Included veinlets forming various loops, and/or reaching the far border of areoles. Included veinlets present in areoles along costa and/or rachis.
    - Polypodium colysoides (irregular form, 95)
    - Pleopeltis p.p. major, see also IVc. (P. angustifrons, 97-98; P. angusta, 149-151; P. astrolepis, 153-154; P. macrocarpa, typically, in adult leaves. 156; P. percussa, 143, 147-148, see also VIa; etc.)
    - Microgramma persicariifolia (casually, recurrent included veinlets present. 236) Campyloneurum spp. (C. angustifolium, see also IVc, 264; etc.)
    - Phlebodium, see also IVc. (P. aureum, 276-277, 286, 278-279, 282-284; P. decumanum, 287-290)

Pyrrosia spp. (P. lingua, occasionally, 366; P. adnascens, occasionally, 369; etc) Drymoglossum fallax (occasionally, 381)

- IVc. Areoles along the rachis and/or costa lacking included veinlets.
  - Schellolepis arguta (irregular form, 118)
  - Polypodium colysoides (occasionally, 95-96)
  - Pleopeltis spp. major., see also IVb. (P. angustifrons, 97–98; P. angusta, 149–150; P. astrolepis, 153–155; P. macrocarpa, 156–157; P. polylepis, occasionally, 159; P. percussa, 146–148, see also VIa; etc.)
  - Microgramma spp. (M. persicariifolia, occasionally, 235–237; M. lycopodioides, in juvenile leaves, occasionally, 213; M. vacciniifolia, occasionally, 240; etc.)
  - Campyloneurum angustifolium (casually, 264)
  - Phlebodium (P. aureum, 267-279, 282-284, 286; P. decumanum, 287-290)
  - Pyrrosia, p.p. major. (P. lingua, 363-366; P. nummularifolia, 372; P. linearifolia, 373-375; etc. see also IVb)
  - Drymoglossum fallax (381)

Polypodiopteris proavita (608, see also VII)

Matoniaceae (Phanerosorus sarmentosus, fertile, casually, 649-650; Matonia pectinata, 647)

V. Reticulate venation: areoles with only recurrent included veinlets in their ontogeny.

Lepisorus (L. thunbergianus, 166–169; L. obscure-venulosus, 180–182; L. subconfluens, 196; L. mildbraedii, 195; etc.)

Neocheiropteris (N. ensata, 303-307; N. phyllomanes, etc.)

Tricholepidium (T. normale, in marginal areoles)

Lemmaphyllum (L. microphyllum, 321, 323-325, 326; L. carnosum; etc.)

Weatherbya accedens (in marginal areoles)

Paragramma longifolia (in marginal areoles, 333-334)

Belvisia (B. callifolia, 340-343; B. mucronata, 352-354; etc.)

Drymoglossum piloselloides (in marginal areoles, 378–379)

Microsorium (including Phymatodes) (M. punctatum 411; M. scolopendrium, 406-409; M. vieillardii, 413, 398-399; M. fortunei, 389-392; etc.)

Diblemma (in marginal areoles, 414)

Leptochilus axillaris (in marginal areoles, 415-416)

Paraleptochilus decurrens (in marginal areoles, 417-419)

Colysis (C. hemionitidea, 427-429; C. pothifolia, 438-440; etc.)

Dendroglossa (D. minor, 444; D. minutula; etc.)

Lecanopteris (including Myrmecophila) (L. carnosa, 541-545; L. sinuata, in marginal areoles; etc.)

cf. Cheiropleuridaceae (Cheiropleuria bicuspis, 661-662) Dipteridaceae (p.p.?)

VI. Reticulate venation; included veinlets irregular in direction.

VIa. Excurrent included veinlets predominant.

Pleopeltis spp. minor (P. polylepis, causually, 158; P. percussa, casually, 144; etc.)

- Campyloneurum sp. (C. angustifolium, 259, 262)
- Drynaria sp. (D. propinqua, 506-509)

Crypsinus spp. (C. pyrolifolius, 572; C. enervis, 566–567; C. taeniatus, 569–570, 573–574; C. lagunensis, C. ebenipes, 576; C. albido-squamatus, 577, 580; etc.)

Pycnoloma (P. metacoelum, 584; P. murudense, 585; etc.)

Loxogramme sp. (L. duclouxii, 617–619; etc.)

VIb. Recurrent included veinlets predominant. Platycerium (in juvenile leaves, 10-12, 23-25) Polypodium (Microgramma?) megalophyllum (198) Pessopteris crassifolia (in marginal areoles, 265-266) Photinopteris speciosa (in juvenile leaves, 485-489) Drynaria spp. (in juvenile leaves, D. quercifolia, 497-499; D. sparsisora, 518-523; D. rigidula, 529-534; etc.) Crypsinus spp. (in juvenile leaves, C. hastatus, 559-565; in marginal areoles, C. engleri,

C. crucifrons; etc.)

Grammatopteridium (G. costulatum, in marginal arcoles, 586; G. brooksii) Selliguea sp. (S. feei, 598–599)

Arthromeris sp. (A. wallichiana, 605–606; etc.) Loxogramme sp. (in juvenile leaves, L. salicifolia, 613-616) VIc. Both excurrent and recurrent included veinlets common. Microgramma spp. (M. persicariifolia, 235, see also IVb; M. lycopodioides, 212, 214; etc.) Pyrrosia spp. (P. shearerii, 376-377; etc.) Pseudodrynaria coronans (in juvenile leaves, 454-459) Aglaomorpha sp. (A. meyeniana, in juvenile leaves, 470-474) Crypsinus spp. (C. taeniatus var. borneensis, 575; etc.) Selliguea spp. (S. heterocarpa, 590–597; S. lima, 601–603; etc.) Arthromeris spp. (A. lehmanii, 607; etc.) Loxogramme spp. (L. nidiformis, 631; L. forbesii; etc.) Reticulate venation: included veinlets distinctly reduced or simplified. Lemmaphyllum sp. (L. microphyllum, 328) Drymotaenium miyoshianum (330-331) Microsorium sp. (in costal areoles, 411) Drynariopsis and other Drynarioid ferns (in costal areoles, 445; etc.) Crypsinus albido-squamatus (in narrow pinna, 581) Pycnoloma (in costal areoles, 583-585) Holcosorus bisulcatus (588-589) Polypodiopteirs proavita (608) Loxogramme spp. (L. conferta, 623-624; L. lankokiensis, 626-628; L. subselliguea. 633-634; etc.)

VII.

Venation patterns are variable in the following genera: Polypodium, Phlebodium (in these genera there are only excurrent included veinlets, and variations appear especially in the taxa of the Neotropics), Microgramma, Pleopeltis (these are mainly Neotropical, both excurrent and recurrent included veinlets are present), Pyrrosia, Crypsinus, Arthromeris, part of Drynaria (these are Paleotropical, both excurrent and recurrent included veinlets are present), Loxogramme (mainly Paleotropical), and Drymoglossum (two quite different types of venation are found within the genus).

### Juvenile plants used in this study

(Species, origin of spores or plants, and voucher specimens)

Pyrrosia lingua (Figs. 356-365), Kyoto city, MITSUTA A-74. Microsorium (Phymatodes) fortunei (382-392), Cult. in Kyoto University Botanical Garden, MITSUTA S-561. M. vieillardii (393-399), New Caledonia, MITSUTA S-792. M. scolopendria (400-410), Cult. in Kyoto University Botanical Garden, MITSUTA S-377. Colysis hemionitidea (420-429), Cult. in Kyoto University Botanical Garden, MITSUTA S-223. C. pothifolia (430-441), Cult. in Kyoto University Botanical Garden, MITSUTA S-191. Pseudodrynaria coronans (446-459), Cult. in Kyoto University Botanical Garden, MITSUTA S-134, S-230. Aglaomorpha meyeniana (460-475), Cult. in Atagawa Botanical garden, Shizuoka pref., MITSUTA S-642. Photinopteris speciosa (478-489), Kisaichi Botanichi Garden, Osaka pref., MITSUTA S-193. Drynaria quercifolia (490-502), Higashiyama Botanical Garden, Nagoya city, MITSUTA S-162. D. propinqua (503-512), Cult. in Montreál

Botanical Garden, Canada, MITSUTA S-699. D. sparsisora (513-523), Montreál Botanical Garden, Canada, MITSUTA S-691. D. rigidula (524-534), Cult. in Kyoto University Botanical Garden, MITSUTA S-43, S-330. Lecanopteris carnosa (535-546), Higashiyama Botanical Garden, Nagoya city, MITSUTA S-155, S-198. Crypsinus hastatus (551-562), Uji city, MITSUTA S-155, S-198. Crypsinus hastatus (551-562), Uji city, Kyoto pref., MITSUTA A-64. C. enervis (566), Luzon, IWATSUKI et al. P-576. Loxogramme salicifolia (609-616), Owase city, Mie pref., MITSUTA S-225. L. duclouxii (617-619), Kyoto city, MITSUTA A-20. L. grammitoides (620-622), Ashiu, Kyoto pref., Cheiropleuria bicuspis (654–664), Miyama-choh, Mie pref., MITSUTA A-67. Tectaria simonsii (665–673), Cult. in Kyoto University Botanical Garden, MITSUTA S-182, S-237. T. decurrens (674-682), Cult. in Atagawa Botanical Garden, MITSUTA S-646. Hemigramma decurrens (683-689), Taiwan, MITSUTA S-924. Quercifilix zeilanica (693-700), Higashiyama Botanical Garden, Nagoya city, MITSUTA S-150, S-176. Pleocnemia irregularis (703-710), Luzon, MITSUTA Tectaria gemmifera (711-720), Cult. in Kyoto University Botanical Garden, MITSUTA S-469. S-704. T. pseudo-sinuata (721-728), New Caledonia, MITSUTA S-874. Ctenitis eatonii (729-735), Cult. in Kyoto University Botanical Garden, MITSUTA S-259. C. subglandulosa (736-742), Cult. in Kyoto University Botanical Garden, MITSUTA S-38, S-39. Lastreopsis sp. (743-749), Queensland, MITSUTA S-488, 490.

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