

## Studies in the Venation and Systematics of Polypodiaceae

### I. Venation (1)

by

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### Introduction

Polypodiaceae in the strict sense is a family of higher leptosporangiate ferns with about 1100 species in more than fifty genera. Its taxonomy, systematic position and distribution were reviewed recently by DE LA SOTA (1973a) and JARRETT (1980), and there are numerous other papers dealing with the taxonomy of this family, though we are still far from a standard generic system.

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 However, these characters are still insufficiently known, being mostly based on outdated and/or fragmentary information.

Venation is one of the most important features for defining the genera of polypodiaceae. The most complicated venation pattern found in Polypodiaceae is considered to have evolved with the simplicity of frond construction, and the less complicated pattern of venation in *Polypodium* is usually considered to be a result of reduction (HOLTUM, 1955; COPELAND, 1947). This evolutionary comparison is, however, the result of speculation based on the comparison of venation patterns found in mature leaves. The stages of development of the venation pattern has seldom been observed for Polypodiaceae. It is generally known that the serial changes in the venation at various developmental stages of the juvenile fronds is useful for recognizing the interrelationship of the venation patterns. Recently, the study of juvenile plants was used for the analysis of venation pattern in *Thelypteris* (IWATSUKI, 1962), *Bolbitis* (HENNIPMAN, 1977), and *Cyrtomium* (MITSUTA, 1977), and also for the analysis of foliar dichotomy in relation to the venation pattern (WAGNER, 1952).

In Polypodiaceae, the serial development of the venation in juvenile plants has been observed for only a few species (WAGNER, 1952; NAYAR, 1963, 1965, 1968; KONTA 1978). In this study I have observed the development of venation for as many genera as possible of Polypodiaceae, and also for some genera of other fern families for the sake of comparison. Comparative observations were made among the families which were considered to have possible affinities to Polypodiaceae, and with Dryopteridaceae subfam. Tectarioideae, as the latter seems to have some venation similar to that of Polypodiaceae. In the following sections, the venation pattern will be described with special attention to juvenile forms for most of the genera of Polypodiaceae. Additional descriptions will be given in the succeeding report of the venation patterns for some other genera of leptosporangiate ferns. Generic classification will be critically discussed based on the observations made here.

#### Acknowledgements

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To Dr. M. Hotta, Dr. H. Koyama, Mr. G. Murata, Dr. M. Kato, and other colleagues of the Department of Botany, I wish to express my cordial thanks for their valuable criticisms and advice. I am also greatly indebted to the curators of many botanical gardens, especially the late Mr. W. Kimura of Atakawa Botanical Garden and Mr. I. Sakanashi of Higashiyama Municipal Botanical Garden, Nagoya city, and also to the operators of spore exchanges, especially Messrs. N. D. Hall, R. F. Cartright, Drs. R. Yoroï and T. Sato. Prof. Y. Sasaki of Kobe Gakuin University, and Dr. F. KONTA of Shizuoka University kindly lent me their important specimens.

Many juvenile plants were cultivated in the greenhouse of the Department of Botany, Kyoto University. I would like to express my special appreciation to the gardeners, especially to Mr. H. Nishimura, for his horticultural assistance. The manuscript was read for linguistic correction by Mr. M. G. Price to whom I am very grateful.

#### Materials and Methods

In the present study, the family Polypodiaceae is circumscribed as in Pichi Sermolli (1958), and the genera included in the family, in their circumscription and arrangement, are mainly based on Copeland (1947) with exceptions stated in the text.

Juvenile plants used in this study were mostly raised from spores, which were collected by myself and/or with the help of many botanists as well as by exchange, and cultivated in the greenhouse of the Department of Botany, Kyoto University, under uniform conditions (voucher specimens with S-). Some juvenile plants were collected in the field alongside the mature plants (voucher specimens with A-).

Venation of the juvenile leaves was observed and drawn after bleaching and staining by acetocarmine. A few drops of a detergent were added prior to bleaching when necessary. When the venation of the juvenile leaves varied among individuals, several forms were shown even at the same stage, especially for the first leaves, for the sake of comparison. In observing the venation in this study, organogenetic development or morphogenetic changes were not actually followed but recognized by the comparison of heteroblastic series of juvenile leaves.

Dried specimens were also examined in the Herbarium of Kyoto University (KYO) for further comparative studies of the adult leaves.

### **Description of venation with special attention to the developmental stages of juvenile plants (1)**

In this chapter, the venation is described and figured for each of 23 genera of the Polypodiaceae. Much effort has been made to observe the developmental formation of venation as seen in heteroblastic series.

#### **Christiopteris COPEL.**

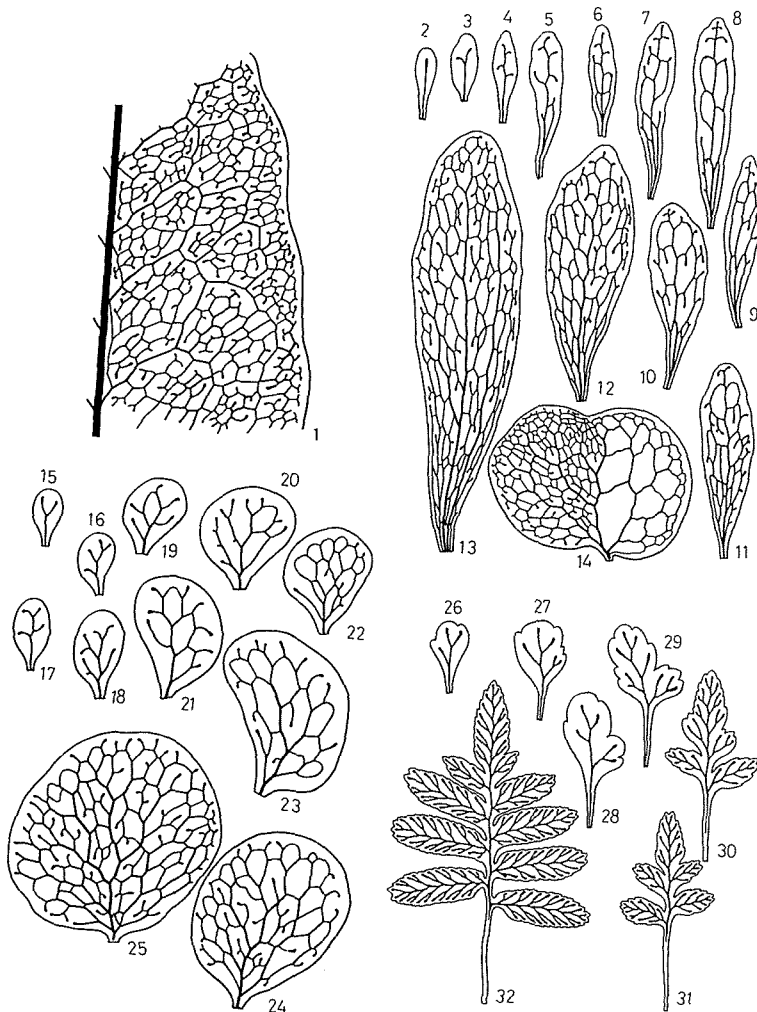
The venation of juvenile leaves has not been previously described for this genus. Branching of mature fronds was reported by BOWER (1923, 1928) for *Christiopteris tricuspis* (HOOK.) CHRIST. In this study, venation of mature fronds was observed for *C. varians* (METT.) COPEL., *C. sagittata* (CHRIST) COPEL. and *C. tricuspis*.

Fronds are usually sagittate (*C. sagittata*, *C. tricuspis*), pedate (*C. tricuspis*, occasionally), or pinnatifid (*C. varians*) with broad leaflets. Veins are anastomosing with irregular included veinlets.

In *C. varians*, smaller costal areoles have mostly recurrent free veinlets only, especially towards the tips of the leaflets. The included veinlets of outer areoles are pointed in various directions. At the middle part of the leaflet, lateral veins form large islets of costal areoles (Fig. 1). Veins are often free at the very margin of the leaflet. Venation of *C. sagittata* and *C. tricuspis* is similar to that of *C. varians*, but the lateral veins are conspicuous and run more strictly parallel to each other.

**Platycerium** DESV.

The venation of the later juvenile leaves was observed by BOWER (1928) for *P. veitchii* (UND.) C. CHR., and by STOKEY and ATKINSON (1954) for the first leaves of *P. alcorni* (WILMET.) DESV.; that of the adult leaves has been observed by various authors, by BOWER (1928) for *P. angolense* WELW. and *P. aethiopicum* HOOK., by



Figs. 1-32. 1: *Christiopteris varians*, lamina of adult leaf. 2-14: *Platycerium bifurcatum*, juvenile leaves. 15-25: *Platycerium grande*, juvenile leaves. 26-32: *Polypodium vulgare*, juvenile leaves.

HOLTUM (1955) for *P. coronarium* (KOENIG) DESV. In this study, observations were made for both juvenile and adult leaves of *P. bifurcatum* (CAV.) C. CHR. (Figs. 2–14) and *P. grande* (J. SM. ex FÉE) KUNZE\* (Figs. 15–25).

The first leaf of *P. bifurcatum* is spatulate, with simple (2), forked (3), or rarely pseudo-monopodial veins (4) according to the size of the leaf, as reported by STOKEY and ATKINSON (1954) for *P. alpicorne*. Lateral veins from the pseudo-monopodial mid-vein of the juvenile leaves of *P. bifurcatum* are slightly recurved. Bifurcation of these lateral veins occurs in the succeeding leaves, and they anastomose (5–9). The areoles usually lack included veinlets. The mid-vein is unbranched and rather prominent in these leaves. Included veinlets were noted in the leaves of various developmental stages where the basiscopic branch of primary, bifurcated lateral veins ends while the forward (upward) one bifurcates again and forms an areole (9–11). This retrorse included veinlet sometimes run to the neighbouring lateral vein, forming a secondary areole without included veinlets (11–12). Excurrent or irregular included veinlets may also be formed. In the succeeding leaves, the single mid-vein becomes obscure, and two (or more) thick veins (plural main-veins) are formed (13). A nest leaf appears at this stage, having similar but roundish areoles. No intermediate form between protruding and nest leaves was observed.

The venation of the juvenile leaves of *Platynerium grande* (Figs. 15–25) is similar to that of *P. bifurcatum*, but *P. grande* has only nest leaves in juvenile plants except for the first and some undifferentiated leaves. Most protruding leaves of this species are fertile. The tip of each veinlet is swollen in juvenile leaves.

The venation of the adult leaves of *Platynerium* is similar for both species, with several-times bifurcated main-veins and minute areoles containing hooked, irregular included veinlets as reported by many authors.

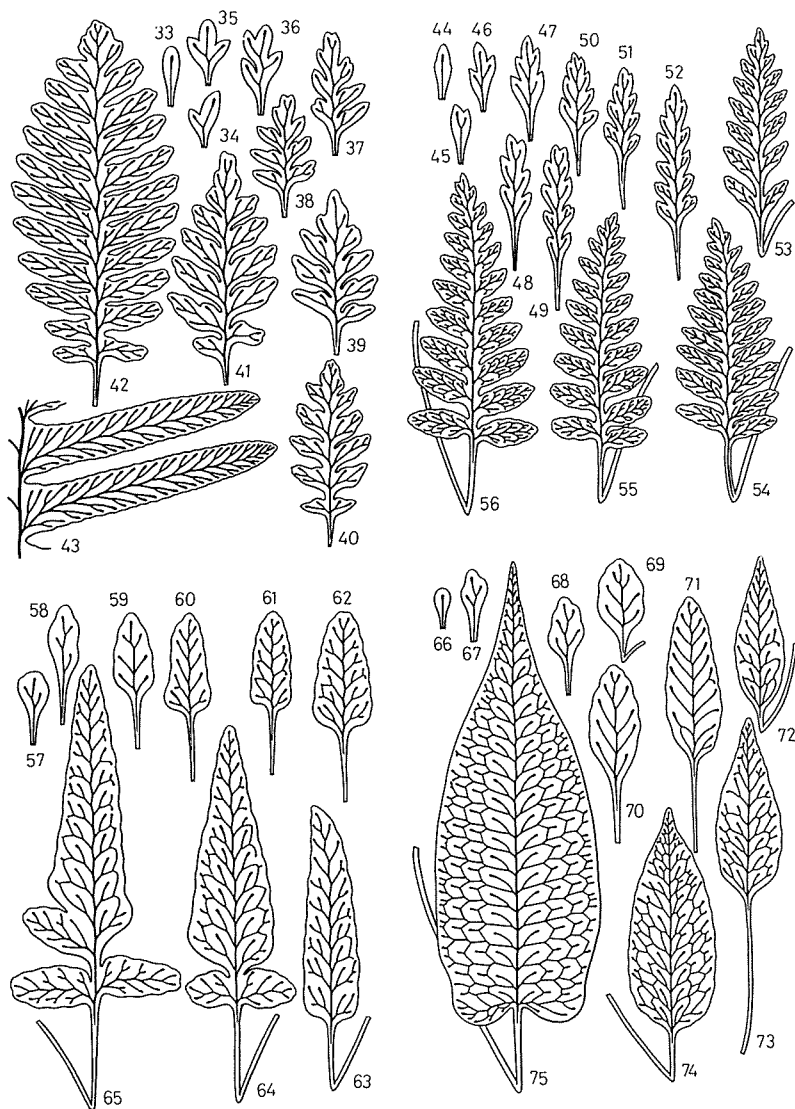
### Polypodium L.

Juvenile plants of *Polypodium* were studied by MITSUTA (1977 for *P. triseriale* Sw., 1981 for *P. glaucophyllum* KUNZE). In the present study, the juvenile leaves of the following species were observed: *P. vulgare* L., *P. plumula* HUMB. et BONPL. ex WILLD., *P. formosanum* BAK., *P. chnoodes* SPRENGEL, *P. glaucophyllum*\*\* , and *P. fallax* SCHLECHT et CHAM.

Juvenile leaves of *Polypodium vulgare* are as follows (Figs. 26–32): veins are usually dichotomous or pseudo-monopodial for the first leaves (26). In the succeeding leaves, the lower lateral vein is always most developed, becoming pinnate (27–31).

\* Although usually attributed to PRESL, Epim. Bot. 154. 1851, this combination was first made by KUNZE, *Linnaea* 23: 274. 1850 (—M. G. PRICE).

\*\* Although this species more or less has aspects of *Campyloneurum*, was treated here under *Polypodium* tentatively.



Figs. 33-75. 33-43: *Polypodium plumula*. 33-42: juvenile leaves. 43: nearly adult leaf. 44-56: *Polypodium formosanum*, juvenile leaves. 57-65: *Polypodium chnoodes*, juvenile leaves. 66-75: *Polypodium glaucophyllum*, juvenile leaves.

The secondary veins from the costule are at first nearly dichotomous (32). Vein tips nearly reach the margin in sterile leaves. Marginal serration or notching corresponds to these veinlets.

Juvenile leaves of *Polypodium plumula* (Figs. 33–43): the first leaf is spatulate with a simple vein (33) or forked with a single veinlet in each lobe (34, 35). Lateral veinlets (costules) are often simple even when several pinnatifid segments are formed (37–41). During these stages, the lowest segment becomes reduced. Bifurcation of the secondary veinlets occur when about 10 pairs of lateral segments are formed (42). Tips of veinlets are swollen and each enters a serration or undulation.

Juvenile leaves of *Polypodium formosanum* (Figs. 44–56): the first leaf is usually simply forked (45, 46) or rarely spatulate with a simple vein (44). Lateral veins from the pseudo-monopodial mid-vein begin to fork as the margin of the leaf becomes dissected (47–52). Bifurcation of lateral veinlets (costules) follows (53, 54). These forked veinlets sometimes anastomose with each other, or the basal acroscopic veinlet may be included in the anastomosis formed by the basal basisopic veinlet and the second acroscopic veinlet (55, 56). Beyond these areoles there are forked free veinlets near the margin. They repeatedly fork and anastomose to forming areoles without included veinlets. A similar pattern can be observed for *P. chnoodes* (Figs. 57–65).

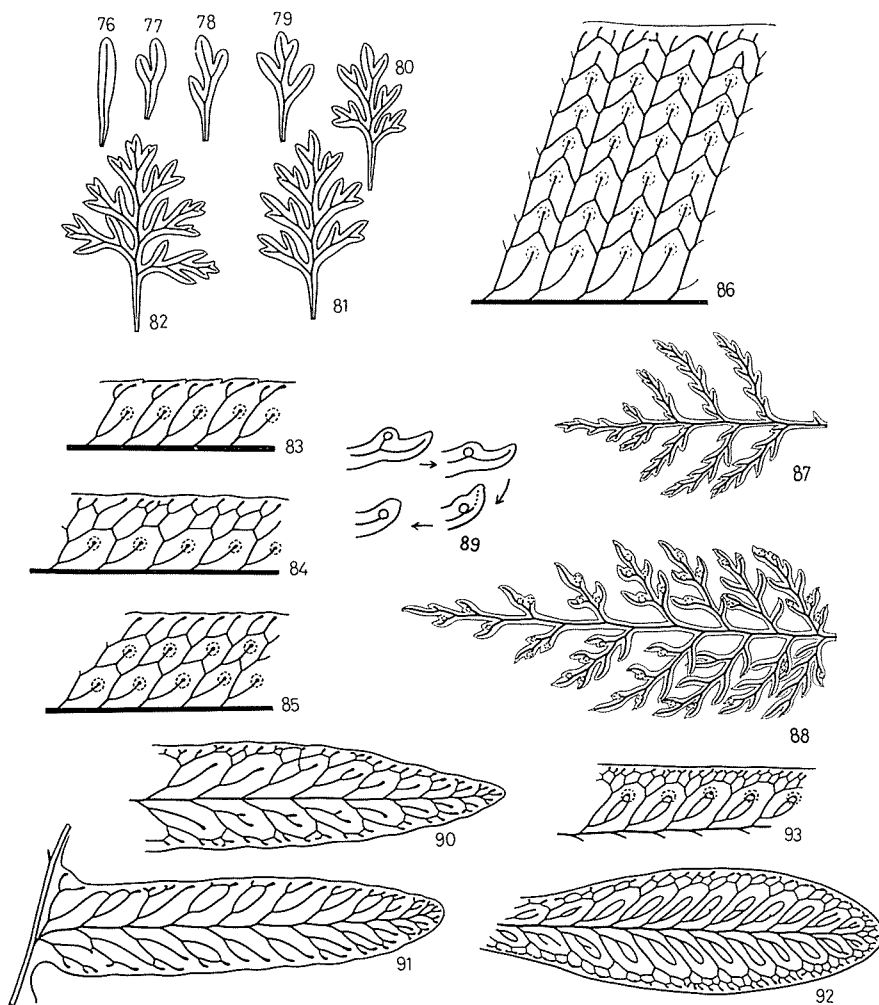
Juvenile leaves of *Polypodium glaucophyllum* (Figs. 66–75): the first leaves are spatulate with veins simple (66) or forked (67). Veins of the juvenile leaves are free at first, and lateral veins are mostly simple until a straight mid-vein is formed (68–71). The basal acroscopic veinlet begins to be included (72, 73) as in *P. chnoodes*. Two rows of areoles at each side of the mid-vein are formed, the outer ones sometimes lacking included veinlets (74). More rows of areoles are added in the later leaves (75). The leaf-margin is often undulate in juvenile leaves, but entire in adult ones.

Juvenile leaves of *Polypodium fallax* (Figs. 76–82): the first leaf is usually simple and lanceolate with a single vein, or forked with a single veinlet in each lobe. The mid-vein is pseudo-monopodial and lateral veins fork in the succeeding leaves, but each single veinlet enters a single lobe. Fig. 82 is of a nearly adult leaf.

The venation and frond form of juvenile plants of the 6 species described above are different from each other: the finely dissected *Polypodium fallax* has a single veinlet in each lobe. On the other hand, the frond is simple and veins are highly anastomosing in *P. glaucophyllum*. The other 4 species are intermediate in those respects. In anastomosing venation, the basal acroscopic veinlet is an excurrent included veinlet, which is mostly simple in this genus. Marginal serration or notching is rather common in these species.

#### Venation of adult leaves

The venation of *Polypodium vulgare* is free in adult leaves (Fig. 83). The basal acroscopic veinlet is shortened when it is soriferous. The adult leaves of *P. glaucophyllum* (Fig. 86) have one of the most highly anastomosed venation within the genus. There are up to 7 rows of areoles at each side of the costa, each areole containing



Figs. 76-93. 76-82: *Polypodium fallax*, juvenile leaves. 83: *Polypodium vulgare*, part of pinna. 84: *Polypodium formosanum*, part of pinna. 85: *Polypodium chnoodes*, part of pinna. 86: *Polypodium glaucophyllum*, part of leaf. 87-89: *Polypodium lindenianum*. 87-88: lateral pinna of sterile and fertile frond. 89: various soral positions, diagrammatically shown. 90: *Polypodium myriolepis*, part of lateral pinna. 91: *Polypodium polypodioides*, lateral pinna. 92-93: *Polypodium (Microgramma) munchii*, part of sterile (92) and fertile pinna (93).

a single, simple, excurrent veinlet. Sori are borne at the tip of these included veinlets. Intermediate venation types between those of *P. vulgare* and *P. glaucophyllum* can be seen in such species as *P. formosanum* (Fig. 84), *P. chnoodes* (85), *P. (Schellolepis)*



*fraxiniifolium* JACK (114, 115) and *P. (S.) caceresii* SOD (116, 117). These variations can also be observed in the juvenile leaves of *P. glaucophyllum*.

Adult leaves of *Polypodium lindenianum* KUNZE (*P. friederichsthalianum* KUNZE) are tripinnate (Figs. 87–89). Each segment of the frond has a single veinlet. Venation is anadromous (87), as is common to the *Polypodium* species, but the basal acroscopic veinlet is sometimes vestigial or lacking, giving an appearance of catadromous branching in some cases (88). Sori are apparently dorsal on veinlets (88), but this is caused by the reduction of soriferous veinlets (89). In spite of its peculiar appearance, the venation of *P. lindenianum* is comparable to that of *P. fallax* (82) and *P. vulgare* (83).

Although the included veinlets are single and simple in the species with reticulate venation mentioned above, forked and/or plural excurrent included veinlets were observed in the following species: *Polypodium myriolepis* CHRIST (American tropics), *P. munchii* CHRIST (*Microgramma*, COPEL., American tropics), *P. ensiforme* THUNB. (South Africa) and *P. colysoides* MAXON et COPEL. (American tropics).

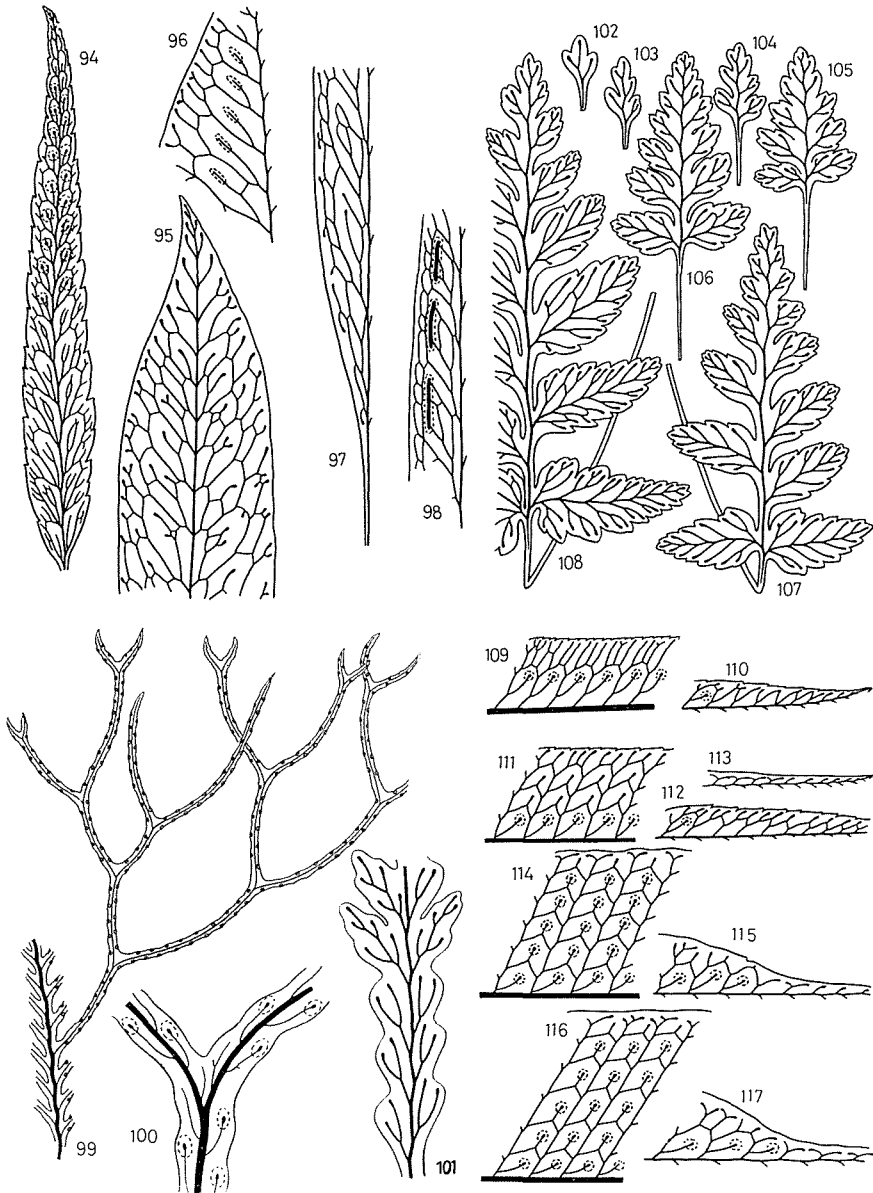
In *Polypodium myriolepis* (Fig. 90), the excurrent included veinlet is often forked, and one of the forks sometimes joins an adjacent vein to form a secondary areole without included veinlet. In the related *P. polypodioides* (L.) WATT. (Fig. 91), lateral segments of sterile fronds often show incompletely anastomosed venation. This species represents a type intermediate between free and typically reticulate venation.

In *Polypodium munchii* (Figs. 92, 93), excurrent included veinlets are often forked, the forks rejoining to form a loop. Each forked veinlet sometimes forks again and bears an included veinlet or two smaller islets within the loop. Sori are borne at the tips of the loops. A loop may be divided into two islets (93).

In *Polypodium ensiforme* (Fig. 94), a forked included veinlet sometimes forms a loop, with an excurrent veinlet outside the islet. Sori are borne at tips of included veinlets as long as they are simple, or dorsal on the basisopic veinlet of forked pairs.

Irregular included veinlets were also observed in *Polypodium colysoides* (Figs. 95, 96). The included veinlets of sterile fronds are sometimes single and simple as common in *Polypodium*, or sometimes forked, the inner (acroscopic) fork two running parallel to the costa and anastomosing with the next veinlet, resulting in areoles without included veinlets along the costa. Plural included veinlets in the same areoles are sometimes united with each other. Venation of the fertile frond is simpler. Sori are elongate, and borne on the terminal part of the included veinlet (96).

Those species with forked and/or plural included veinlets mentioned above are distributed in the New World and/or Africa. Asian and European species of *Polypodium* are uniform in having simple included veinlets, except for the case of some



Figs. 94–117. 94: *Polypodium ensiforme*, fertile lateral pinna. 95–96: *Polypodium colysoides*, part of sterile (95) and fertile pinna (96). 97–98: *Pleopeltis angustifrons*, part of frond. 99–101: *Polypodium fucoides*, part of frond (99) and enlarged (100–101). 102–110: *Schellolepis arguta*. 102–108: juvenile leaves. 109–110: part of lateral pinna, fertile. 111–113: *Schellolepis persicifolia*, part of lateral pinna, fertile. 114–115: *Polypodium fraxinifolium*, part of lateral pinna, fertile. 116–117: *Polypodium caceresii*, part of lateral pinna.

*Schellolepis* mentioned in the following chapter.

Repeatedly forked pinnae are known for *Polypodium fucoides* CHRIST (Figs. 99–101). Sori are borne at the tips of simple or forked veinlets (100). Veins are all free. Lobes sometimes develop with pseudo-monopodial veins (101). Typical bifurcations are observed only with the main vein (costa) of lateral pinna, as is often observed in some cultivated forms of *Nephrolepis* and *Phyllitis scolopendrium* (L.) NEWM.

### **Schellolepis J. SMITH**

The venation of the adult leaves of this genus has been studied by various authors including CLARKE (1880), BEDDOME (1883), COPELAND (1947) and HOLTUM (1955). That of juvenile leaves was observed by MITSUTA (1981). In juvenile leaves of *Schellolepis arguta* (WALL. ex HOOK.) J. SM. (Figs. 102–108), veins are free for all the early stages (102–107), then anastomose without included veinlets (108), and ultimately produce a simple excurrent included veinlets in areoles along the costa.

In the adult leaves of *Schellolepis arguta* (Figs. 109, 110), single or incomplete double rows of areoles occur at each side of the costa. In *S. persicifolia* (DESV.) PIC. SER. (Figs. 111–113), venation is similar to that of *S. arguta*, but areoles on each side of the costa are formed in up to three rows. In *S. percussa* (CAV.) PIC. SER. (*Polypodium cyathoides* Sw. Fig. 119), included veinlets are sometimes plural and/or forked in sterile fronds. Each forked or plural included veinlet anastomoses, making a smaller islet in the primary areole. Included veinlets of fertile fronds are usually as typical of *Polypodium*. In *S. arguta*, the included veinlets of sterile fronds are also sometimes forked, with the inner branch nearly parallel to the costa and anastomosing with the next veinlet, resulting in narrow areoles without included veinlets along the costa.

### **Thylacopteris KUNZE apud METT.**

Venation of adult leaves of *Thylacopteris papillosa* (BL.) KUNZE was described by COPELAND (1947) and HOLTUM (1955). The venation of fertile lobes is well illustrated in HOLTUM (l.c.) as *Polypodium papillosum* BL. Venation of juvenile plants has not yet been observed for this species.

Venation of lateral segments of *Thylacopteris papillosa* is simple with a monopodial mid-vein (costa) and forked veinlets (Fig. 120). Both basal acroscopic and basispic veinlets seem usually to depart directly from the rachis except for those in terminal segments, where they are truly catadromous, very unusual for *Polypodium* and its relatives.

### **Dictymia J. SMITH**

Venation of adult leaves of this genus was observed by COPELAND (1947). In juvenile leaves of *Dictymia mckeei* TINDALE (Figs. 121–129), the first leaf is broadly spatulate with a single vein (121). Veins are free in these and succeeding leaves. Lateral veinlets are forked, the basiscopic branch directed downwards. Opposite basiscopic and acroscopic branches anastomose (124, 125). Outside the costal areoles, similar areoles are formed with further branches of primary veinlets (126–128), and no included veinlets. In older leaves, various forms of included veinlets are rare (129 left, central part). Sori are borne on commissures of veins. Tips of veinlets are not swollen.

### **Synammia PRESL**

Venation of adult leaves was described by COPELAND (1947) and others; that of juvenile leaves has not been observed.

In *Synammia feuillei* (BERTERO) COPEL. (Fig. 130), veins are anastomosing, forming a single row of large costal areoles each with a single, simple, excurrent, included veinlet. In some specimens, additional smaller areoles without included veinlets are found outside these large areoles. At the margin occur excurrent free veinlets, the tips of which are swollen and end at the base of serrations.

Sori are dorsal on the terminal part of excurrent included veinlets, elongate in *Synammia feuillei*, or short ellipsoid in *S. intermedia* (COLLA) KUNKEL.

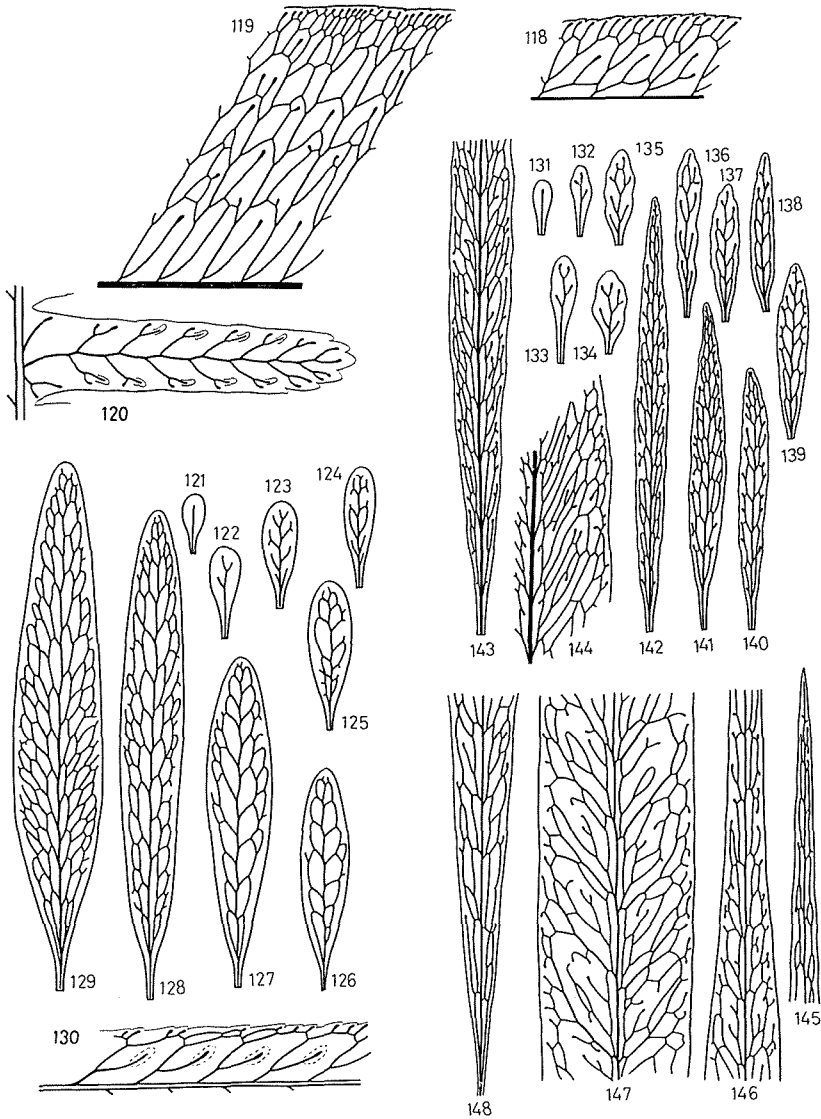
### **Pleopeltis HUMEOLDT et BONPLAND in WILLD. (*Lepisorus* excluded)**

Venation of adult leaves of *Pleopeltis* s. str. was described by VARESCHI (1968) for *P. lanceolata* (L.) KAULF.; that of the juvenile leaves was reported by MITSUTA (1981).

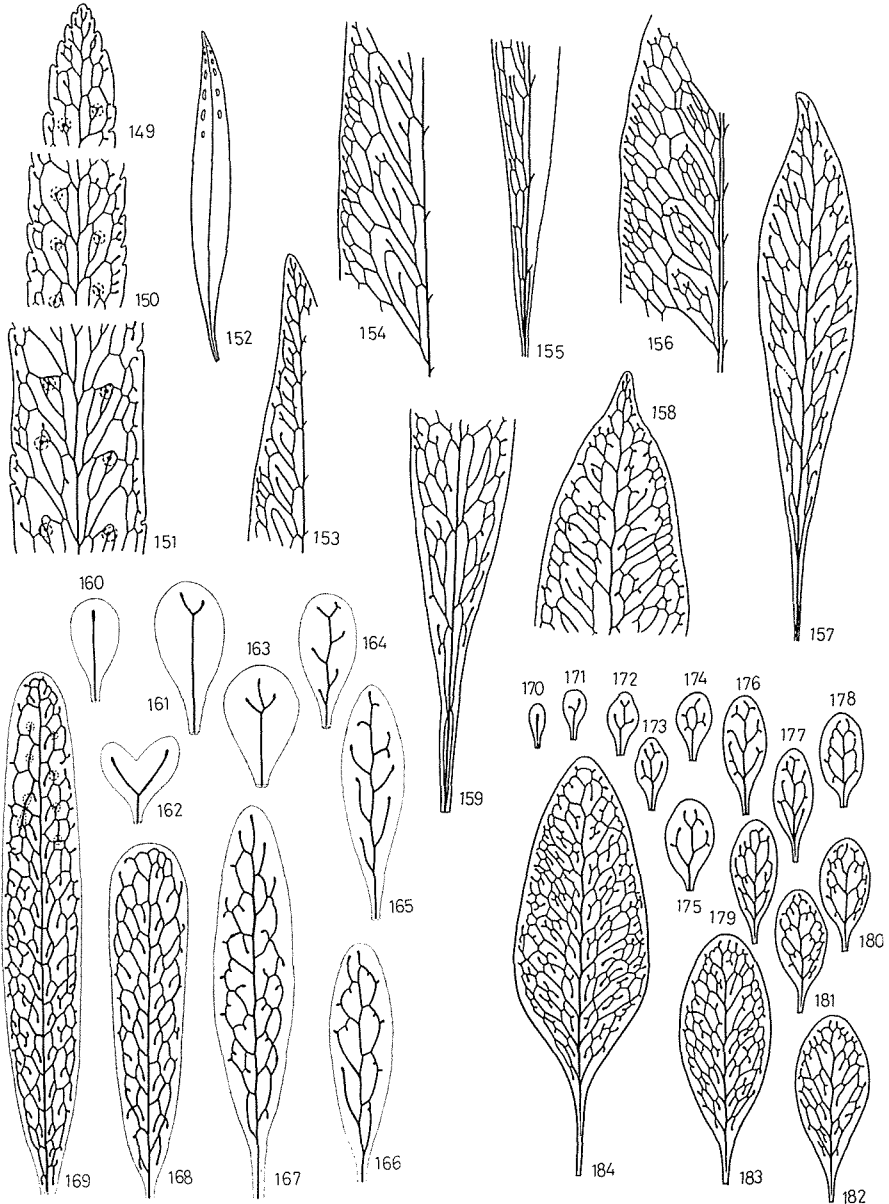
Juvenile leaves of *Pleopeltis percussa* (CAV.) HOOK. et GREV. are as follows (Figs. 131–143): the first leaf is spatulate with simple (131) or pseudo-monopodially branched veins (312). In the succeeding leaves, lateral veinlets are simple (133) or forked (134), both of the opposite branches anastomose (135–138), and narrow areoles are formed along the costa. Outer rows of areoles are added in the same way (139–142). These areoles lack included veinlets (143).

Juvenile leaves of *Pleopeltis percussa* have stellate hairs instead of stellate scales on the adult leaves.

Venation of the adult leaves was observed for *Pleopeltis percussa* (Figs. 144–148), *P. angusta* HUMBOLDT et BONPL. (149–151), *P. astrolepis* (LIEBM.) FOURN. (152–155), *P. macrocarpa* (BORY ex WILLD.) KAULF. (156–157) and *P. polylepis* (ROEM.) MOORE



Figs. 118-148. 118: *Schellolepis arguta*, part of lateral pinna, sterile. 119: *Schellolepis percussa*, part of lateral pinna, sterile. 120: *Thylacopteris papillosa*, lateral pinna, fertile. 121-129: *Dictymia mckeei*, juvenile leaves. 130: *Synammia feuillei*, part of lateral pinna, fertile. 131-148: *Pleopeltis percussa*, 131-144: juvenile leaves. 145-148: adult leaf.



Figs. 149-184. 149-151: *Pleopeltis angusta*, part of lateral pinna, fertile. 152-155: *Pleopeltis astrolepis*, outline of leaf (152) and venations of sterile leaf (153-155). 156-157: *Pleopeltis macrocarpa*, adult (156) and semi-adult (157) leaves, sterile. 158-159: *Pleopeltis polylepis*, adult leaf. 160-169: *Lepisorus thunbergianus*, juvenile (160-168) and small fertile leaves (169). 170-184: *Lepisorus obscure-venulosus*, juvenile leaves.

(158–159). In adult leaves of *P. percussa*, recurrent included veinlets sometimes occur in the narrow areoles along the costa (144). Such recurrent included veinlets are often located between excurrent veinlets. Apical and basal part of the adult leaves (145, 148) have areoles such as seen in the juvenile leaves. Veins are free at the entire margin of the frond, and the tips of veinlets are swollen.

*Pleopeltis angusta* has pinnatifid fronds. At the tip of lateral pinnae there are narrow areoles without free included veinlets. Excurrent included veinlets are observed in the second row of areoles (149). Sori are dorsal on the terminal part of the loop of these excurrent included veinlets. At the base of the pinna, these loops are more complex, reaching the border of outer rows of areoles, and often uniting each other (150–151), resulting in the formation of smaller areoles. Between these excurrent included veinlets are recurrent ones in the narrow costal areoles. Margins are serrate and the veinlets derived from a single lateral vein all go to one lobe between the sinus.

In *Pleopeltis astrolepis* (Figs. 152–155), plural and branched excurrent included veinlets are produced. At the basal part of the frond, veins anastomose without included veinlets

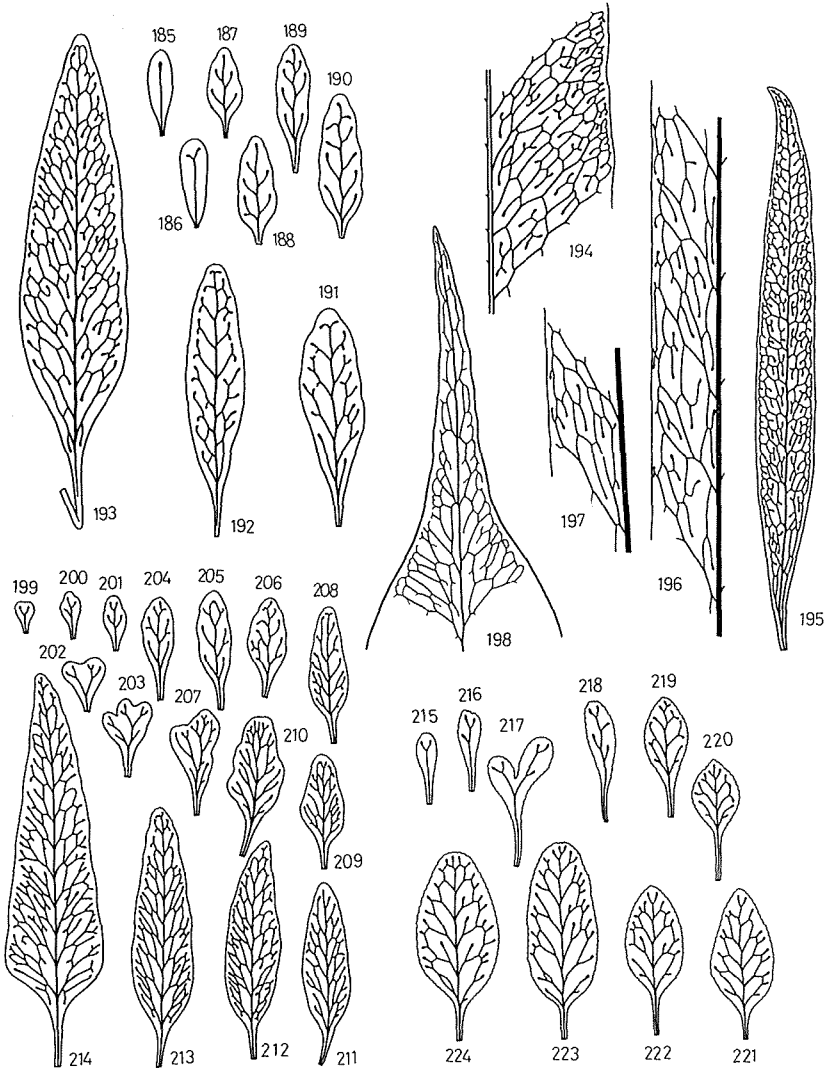
In *Pleopeltis macrocarpa* (Figs. 156, 157), excurrent included veinlets of costal areoles are forked several times, and may be united to each other or extend to the outer border of the areole (156). The basal acroscopic branches of lateral veins sometimes remain free in adult leaves as well as in the juvenile leaves. Marginal areoles are usually small and without included veinlets.

In *Pleopeltis polylepis* (Figs. 158–159), narrow costal areoles often have recurrent included veinlets between the excurrent ones. The basal part of the frond has venation similar to *P. astrolepis*.

### **Lepisorus (J. SMITH) CHING**

Venation of the adult leaves of *Lepisorus* was examined by various authors, including CLARKE (1880), BEDDOME (1883), HOLTUM (1955), BIR and TRIKHA (1968, 1974) and recently by MITSUTA (1981); that of the juvenile leaves was also described with notes for some species by MITSUTA (1981).

Venation of the juvenile and adult leaves of *Lepisorus thunbergianus* is as follows (Figs. 160–169): the first leaf is broadly spatulate or obovate, with simple or forked veins (160, 161). Dichotomous fronds are sometimes found for the first leaf (162). In succeeding leaves, a pseudomonopodial mid-vein is established, and lateral veins become forked (163–165). The basisopic branch is directed downwards and anastomoses with the opposite acroscopic one to form a recurrent included veinlet and an excurrent free branch (166). This excurrent branch then branches and



Figs. 185-224. 185-193: *Lepisorus excavatus*, juvenile leaves. 194: *Lepisorus annuifrons*, part of adult leaf. 195: *Lepisorus mildbraedii*, adult leaf. 196-197: *Lepisorus subconfluens*, part of adult leaf. 198: *Mecosorus (Microgramma?) megalophyllus*, terminal part of leaf. 199-214: *Microgramma (Anapeltis) lycopodioides*, juvenile leaves. 215-224: *Microgramma (Lopholepis) piloselloides*, juvenile leaves.

anastomoses in a similar way, and areoles with recurrent included veinlets are formed outside the costal areoles, resulting in two islets without included veinlets (168, 169). Venation of the adult leaves is similar to that of the juvenile ones. Sori are dorsal



on the apical portion of acroscopic branches of the lateral veins, or on a commissure of veinlets. Tips of veinlets are swollen.

Venation of the juvenile leaves of *Lepisorus obscure-venulosus* (Figs. 170–184) is similar to that of *L. thunbergianus*, though in the former, the lateral veins fork at younger stages (174–176). In larger leaves, recurrent included veinlets of outer rows of areoles branch several times, and some branches are united to the distal border of inner areoles (183, 184). Irregular included veinlets are thus formed in the secondary (smaller) areoles.

The venation of the juvenile leaves of *Lepisorus excavatus* (Figs. 185–193) is similar to that of *L. thunbergianus*.

Variation is observed in the venation of adult leaves. *Lepisorus mildbraedii* (HIERON.) PIC. SER. (Fig. 195) and *L. subconfluens* CHING (Figs. 196–197) have rather simple venation, while that of *L. annuifrons* (MAK.) CHING (Fig. 194) and *L. scolopendrius* (HAM. ex DON) TAGAWA is complex and the primary areoles are divided into many smaller ones. At the apical part of the frond, the latter two species have venation similar to that of *L. thunbergianus* and *L. obscure-venulosus*. This type of complex venation is common to the broader-leaved species.

### Microgramma PRESL

Venation of the adult leaves of *Microgramma* was well described by COPELAND (1947) and DE LA SOTA (1963, 1973a, b). In this study, the juvenile leaves were observed for three species, *M. lycopodioides* (L.) COPEL., *M. piloselloides* (L.) COPEL. and *M. vaccinifolia* (L. & F.) COPEL.

In the juvenile leaves of *Microgramma lycopodioides* (*Anapeltis*, J. SMITH, Figs. 199–214), the first leaf is spatulate to broadly spatulate and has a forked or simple vein (199–202). In the succeeding leaves, lateral veinlets fork, and opposite branches unite to form anastomoses (204–206), leaving excurrent veinlets outside the areoles (212–213). Excurrent veinlets are sometimes enclosed and become included veinlets. The narrow costal areoles usually lack recurrent included veinlets until this stage. In the later leaves, such recurrent veinlets increase in number (214), and they often fork at their apex.

In *Microgramma piloselloides* (*Lopholepis*, J. SMITH, Figs. 215–224), the first leaf is spatulate with a forked or simple vein (215–216). Narrow costal areoles are formed similarly to *M. lycopodioides*, though lateral veins form a wider angle with the costa (218–221). In the succeeding leaves, an excurrent included veinlet appears as the basal acroscopic branch of the lateral vein (222–224). The excurrent included veinlets are at first simple, but often fork in the later (adult) leaves. In *Microgramma vaccinifolia* (*Craspedaria*, J. SMITH, Figs. 225–234), the venation of the juvenile leaves

is similar to that of *M. piloselloides*.

Venation of adult leaves of *Microgramma* is variable. In *M. persicariifolia* (SCHRADER) PRESL (Figs. 235–237), venation is simple at the apical and basal part of the frond. In the middle part, there is a row of narrow areoles along the rachis. Some of them have recurrent included veinlets between or next to the excurrent veinlets (236). At the outer part there are large areoles formed by thick veinlets, which are divided into many smaller areoles with or without included veinlets. Small pentagonal areoles are produced near the distal edge of these large areoles. Outside them, there are many smaller areoles of irregular shape, and they mostly lack included veinlets. There are many free excurrent veinlets with swollen tips approaching but not reaching the margin.

Venation of the adult leaves of *M. lycopodioides* (Figs. 242–243) is similar to that of *M. persicariifolia*, though the included veinlets are more numerous and distinct in the former.

Venation of both *Microgramma piloselloides* (Figs. 238, 239) and *M. vacciniifolia* (Figs. 240, 241) is much simpler, especially in fertile leaves (239, 241). One row of distinct areoles is produced on each side of the costa, and each areole has an excurrent included veinlet bearing a sorus at its apex.

In *Microgramma squamulosa* (KAULF.) DE LA SOTA, venation is intermediate between that of *M. lycopodioides* and *M. vacciniifolia*, similar to the venation of *Pleopeltis macrocarpa* shown in Fig. 156.

Venation of '*Polypodium*' *megalophyllum* DESV. (*Mecosorus* KL., Fig. 198) is very complex and variable. There are narrow costal areoles, usually with one to several recurrent included veinlets. In this characteristic, this species looks like *Lepisorus*, but the tips of the veinlets are not swollen, and the paraphyses are filamentous hair rather than the peltate scales.

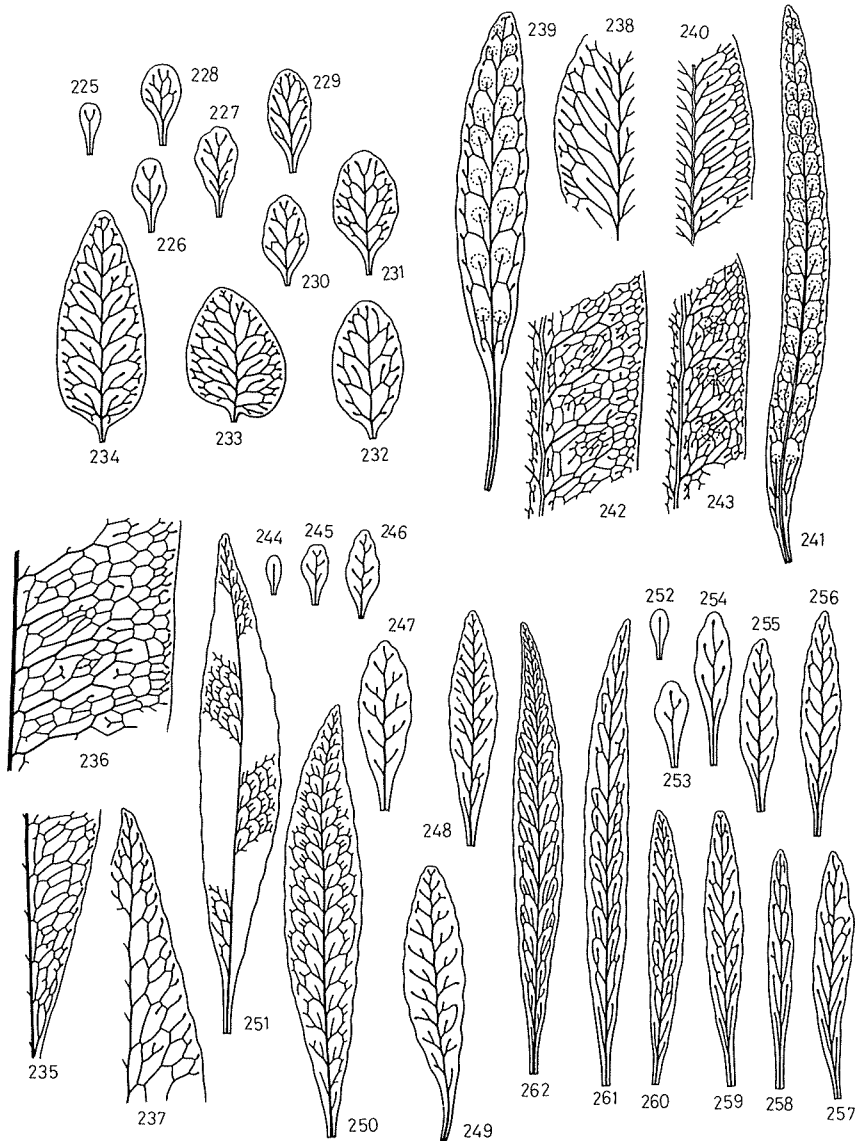
### **Solanopteris COPEL.**

Venation of the adult leaves was described in detail by WAGNER (1972). According to my observations, *Solanopteris brunei* (WERCKLE in CHRIST) WAGNER has costal areoles with recurrent included veinlets only, the tips of which are often hamate and swollen. In the outer rows of areoles, recurrent included veinlets are predominant.

Hair-like scales on the lamina of *Solanopteris brunei* are not clathrate, the usual type in *Polypodium* and *Microgramma*.

### **Campyloneurum PRESL**

Venation of the adult leaves of this genus is known as Venatio *Cyrtophlebii*, and



Figs. 225–262. 225–234: *Microgramma (Craspedaria) vacciniifolia*, juvenile leaves. 235–237: *Microgramma persicariifolia*, part of adult leaf. 238–239: *Microgramma vacciniifolia*, sterile (238) and fertile (239). 240–241: *Microgramma vacciniifolia*, sterile (240) and fertile (241). 242–243: *Microgramma lycopodioides*, sterile (242) and fertile (243). 244–251: *Campyloneurum phyllitidis*, juvenile leaves. 252–262: *Campyloneurum angustifolium*, juvenile leaves.

has been studied by various authors; that of the juvenile leaves was described by MITSUTA (1981) for *Campyloneurum phyllitidis* (L.) PRESL and *C. angustifolium* (Sw.) FÉE.

Venation of the juvenile leaves of *Campyloneurum phyllitidis* is as follows (Figs. 244–251): the first leaf is spatulate with a simple or forked veinlet (244). In succeeding leaves, pseudo-monopodial mid-veins are formed with forked veinlets (245–247). These lateral veins sometimes anastomose (248), and in more developed leaves the basiscopic branches are prolonged (249). In later leaves, branching occurs of the basiscopic branches, and the secondary acroscopic branches are dominant. This is repeated in later leaves, resulting in the anastomosis of the basiscopic and dominant acroscopic veinlets (250–251). Free included veinlets are one or two.

In the juvenile leaves of *Campyloneurum angustifolium* (Figs. 252–262), venation is similar to that of *C. phyllitidis*, but differs in the following respects: lateral veins are at a more acute angle; recurrent included veinlets are found (259, 260, 262); outer areolae have a single excurrent free veinlet or none. The narrow areoles along the costa, often present in the adult leaves (Figs. 263, 264), are not found in juvenile leaves. These areoles are formed in later leaves by the forking and anastomoses of excurrent (acroscopic) included veinlets inside the innermost large areoles.

The venation of *Campyloneurum caudatum* FÉE and *C. vexatum* (D.C. EATON) CHING is intermediate between the two types described above. The former has rather broad fronds and the reniform areoles are usually divided into two by the extension of a middle excurrent included veinlet. Two parallel areoles are thus observed between lateral veins. The latter has lanceolate fronds, with many excurrent included veinlets which often extend outwards and sometimes contain recurrent included veinlets.

### **Pessopteris UNDERWOOD et MAXON**

Venation of *Pessopteris crassifolia* (L.) UNDERW. et MAXON is known as Venatio Anaxetii; that of the juvenile leaves has not been observed as yet.

Venation of the adult leaves of *P. crassifolia* is rather complex (Figs. 265–266). At the apical portion of the frond there are a few rows of areoles at each side of the costa, and the costal areoles have usually single or plural recurrent included veinlets. Outer rows of areoles are smaller, having simple or hamate included veinlets directed irregularly. At the middle part of the frond, there are about 8 rows of areoles on each side of the costa. Outer rows of areoles are reniform to parallelogramiform in outline, and bordered with thick veinlets. These areoles in the outer rows are divided into several smaller ones, each of them usually having forked, irregularly directed, included veinlets. Sori are on the commissure of veinlets, and the tips of

veinlets are conspicuously swollen.

### **Phlebodium (R. BR.) J. SMITH**

Venation of *Phlebodium aureum* (L.) J. SMITH is known as Venatio Phlebodii; that of the juvenile leaves was observed by DE LA SOTA (1963, 1973a) and further by MITSUTA (1981).

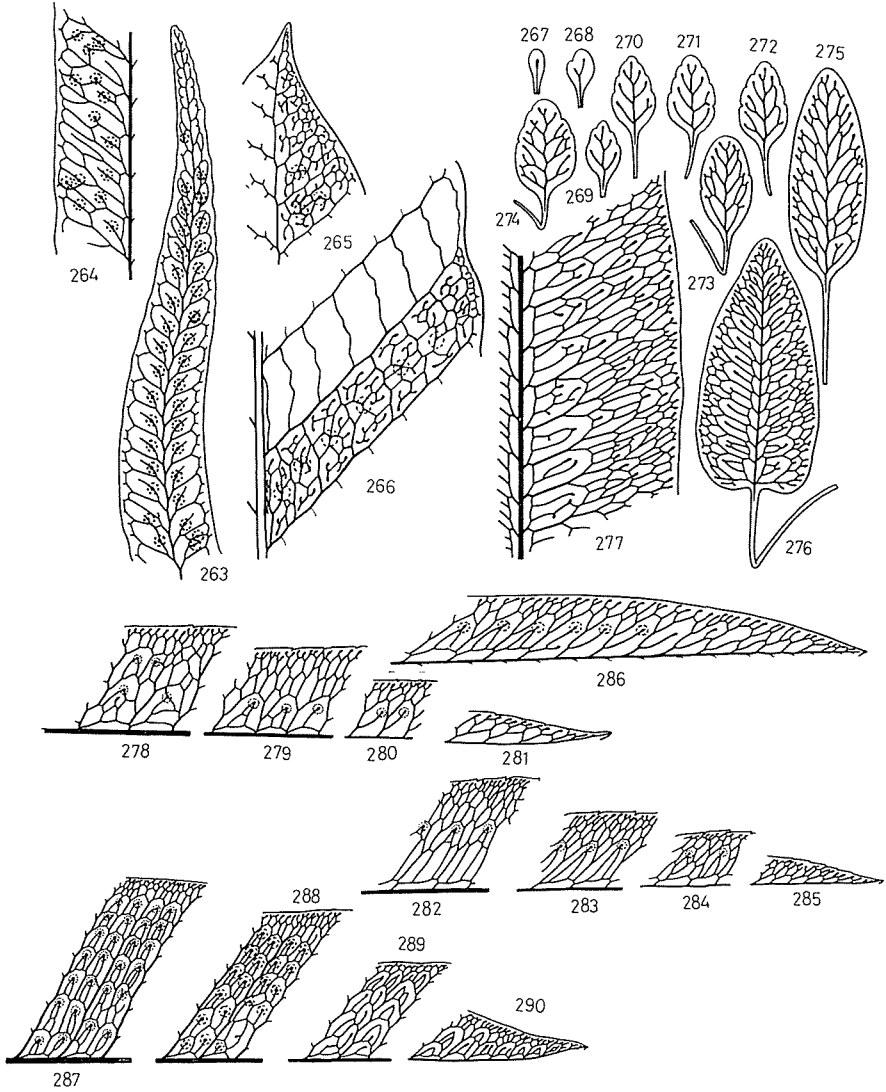
Venation of juvenile leaves of *Phlebodium aureum* is as follows (Figs. 267–276): the first leaf is spatulate with a single veinlet (267) or of various form with a once-forked veinlet (268). A pseudo-monopodial mid-vein is formed in the succeeding leaves (269–271). At this stage, lateral veins are simple or forked and the margins are repand to crenate where approached by lateral veinlets. Both acroscopic and basicopic branches of lateral veinlet anastomose (272, 273). Areoles are at first without included veinlets, and then the basal acroscopic veinlet is included (274, 275). The margin is notched at this stage. Included acroscopic veinlets fork in the succeeding leaves. The tips of acroscopic branches are united to the next lateral veins, and form narrow areoles without included veinlets along the costa. The free branches of the primary acroscopic veinlet run outwards, often forming small areoles by looping inside the large areoles (276). At the outer portion of these large areoles, there are many smaller areoles, some being with excurrent included veinlets. The leaf-margin is entire at this stage, and the tips of the veinlets are distinctly swollen.

Venation of the adult leaves of *Phlebodium aureum* is variable (Figs. 277–286). The commonest type is as shown in Fig. 277, which was drawn from plants raised from spores, and is the same as that of the juvenile leaves described above. Fig. 286 is drawn from *P. aureum* var. *areolatum* (WILLD.) BAK. and is similar to the venation of the juvenile leaves (276). Figs. 278–281 are from a Jamaican plant with roundish areoles. In this material, simple excurrent included veinlets were also observed (280). Figs. 282–285 are from Costa Rican plants and are distinctive in having very narrow areoles. In these materials, main lateral veinlets are not conspicuous and departed from the costa at an acute angle. In all these materials, narrow costal areoles were observed.

In *Phlebodium decumanum* (WILLD.) J. SMITH (Figs. 287–290), two parallel rows of areoles occur between the lateral veinlets (287, 288). At the distal part of the pinnae, these rows are not very distinct (289) or hardly present (290). Fig. 289 is similar to that of *P. aureum* (278), and 290 to 276.

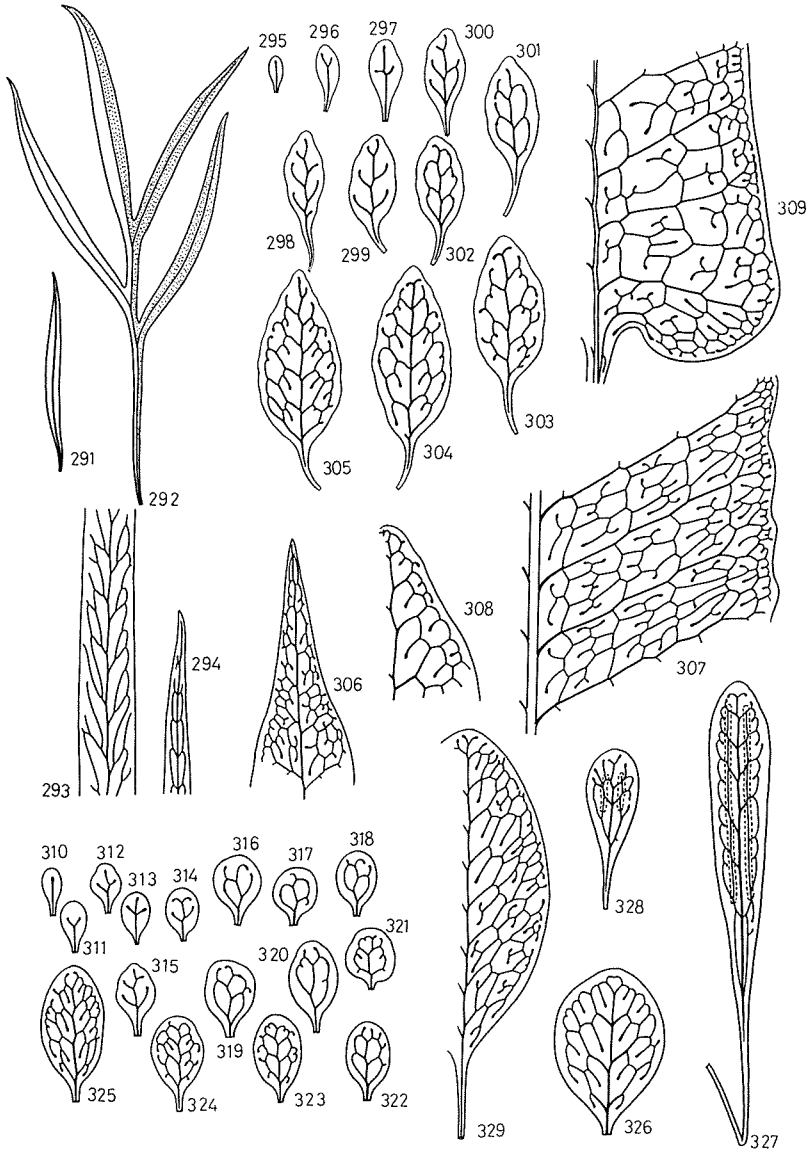
### **Eschatogramme TREVISAN**

Venation of the juvenile leaves has not been observed; that of the adult leaves was described by COPELAND (1947). My observations on *Eschatogramme desvauxii*



Figs. 263-290. 263-264: *Campyloneurum angustifolium*, fertile leaves. 265-266: *Pessopteris crassifolia*, part of fertile leaf. 267-286: *Phlebodium aureum*. 267-276: juvenile leaves. 277: part of adult pinna. 278-281: Jamaican plant, part of fertile pinna. 282-285: Costa Rican plant, part of fertile pinna. 286: *Ph. aureum* var. *areolatum*, part of fertile pinna. 287-290: *Phlebodium decumanum*, part of fertile pinna.

(KL.) C. CHR. (Figs. 291-294) are as follows: fronds are simple to a few times furcate. At the middle of each lateral segment, there is a single row of areoles along the costa, with smaller areoles in some case between them. Both sizes of areoles are without



Figs. 291-329. 291-294: *Eschatogramme (Dicranoglossum) desvauxii*, semi-adult (291) and adult (292) leaves, and venation of 292. Only main-veins are shown for 291 and 292. 295-307: *Neocheiropteris ensata*, juvenile (295-305) and part of adult leaves (306, 307). 308-309: *Neocheiropteris subhastata*, part of adult leaf. 310-329: *Lemmaphyllum microphyllum*. 310-325: juvenile leaves. 326-328: adult leaves, sterile (326) and fertile (327, 328). 329: *L. microphyllum* var. *obovatum*, adult leaf.

included veinlets (293). At the distal part of the segments a single row of very narrow costal areoles is present, or the veins are all free (294). Leaves of semi-adult plants are often simple with free lateral veins. Elongate sori are borne on marginal commissures of the veinlets.

### **Neocheiropteris** CHRIST

Venation of the adult leaves of *Neocheiropteris* was observed by BOWER (1923, 1928) and IWATSUKI (1969); that of juvenile leaves was observed by MITSUTA (1981). Venation of the juvenile leaves of *N. ensata* (THUNB.) CHING is similar to that of *Microsorium* and *Lepisorus* (Figs. 295–305).

In the adult leaves of *Neocheiropteris ensata* (Figs. 306, 307), the venation is so-called Venatio Anaxetii. At the middle portion of leaves, there are several rows of large areoles on each side of the mid-vein (307). The costal areoles have one or two, simple or forked, recurrent included veinlets. Outer rows of areoles are divided into several smaller areoles by connecting veinlets. Each smaller areole usually has a simple or forked included veinlet irregular in direction. In the apical part of the frond (306), there are a few rows of areoles, usually with only recurrent included veinlets. Tips of veinlets are distinctly swollen.

In *Neocheiropteris subhastata* (BAK.) TAGAWA (Figs. 308, 309), the venation is simpler than in *N. ensata*, and recurrent included veinlets are very conspicuous at the broadest part of frond (309) as well as near the apex (308). In *N. sarawakensis* TAGAWA, the recurrent included veinlets in the innermost areoles are forked several times, often anastomosing with the neighbouring ones.

### **Tricholepidium** CHING

Venation of the adult leaves of *Tricholepidium normale* (DON) CHING was observed and illustrated by HOLTUM (1955) as *Microsorium normale* (DON) CHING; that of juvenile leaves has not been observed.

In adult leaves of *Tricholepidium normale*, areoles with broadly cuneate bases are located between the areoles along the costa, in the same way as in *Leptochilus axillaris* (CAV.) KAULF. Otherwise, the venation is similar to that of *Neocheiropteris*, *Lepisorus* and *Microsorium*.

### **Platygyria** CHING et S. K. WU

Venation of three species of *Platygyria* was illustrated by CHING and S. K. WU (1980). According to their figures, the areoles are in up to several rows on each



side of the costa. The innermost ones are very narrow, whereas those of the outer rows are broader. Each areole usually has recurrent or irregular included veinlets.

### **Lemmaphyllum PRESL**

In the juvenile leaves of *Lemmaphyllum microphyllum* PRESL (Figs. 310–325), areoles are formed similarly to *Lepisorus*. Areoles of small leaves sometimes lack included veinlets (316–319).

Areoles without included veinlets were also seen in small fertile leaves (328) and in the innermost row in large fertile leaves (327). In the latter case, even the lateral veins were sometimes partly reduced.

The most complex venation is in large leaves of *Lemmaphyllum rostratum* (BEDD.) TAGAWA which has about four rows of large areoles on each side of the costa.

### **Drymotaenium MAKINO**

The venation of a semi-adult leaf of *Drymotaenium miyoshianum* (MAKINO) MAKINO (Fig. 330) is simply reticulate, usually without included veinlets. In the adult leaves (Fig. 331), one to three rows of very narrow areoles are present at each side of the costa. Inner areoles often lack included veinlets when the leaf is fertile. Tips of veinlets are swollen.

### **Paragramma (BLUME) MOORE**

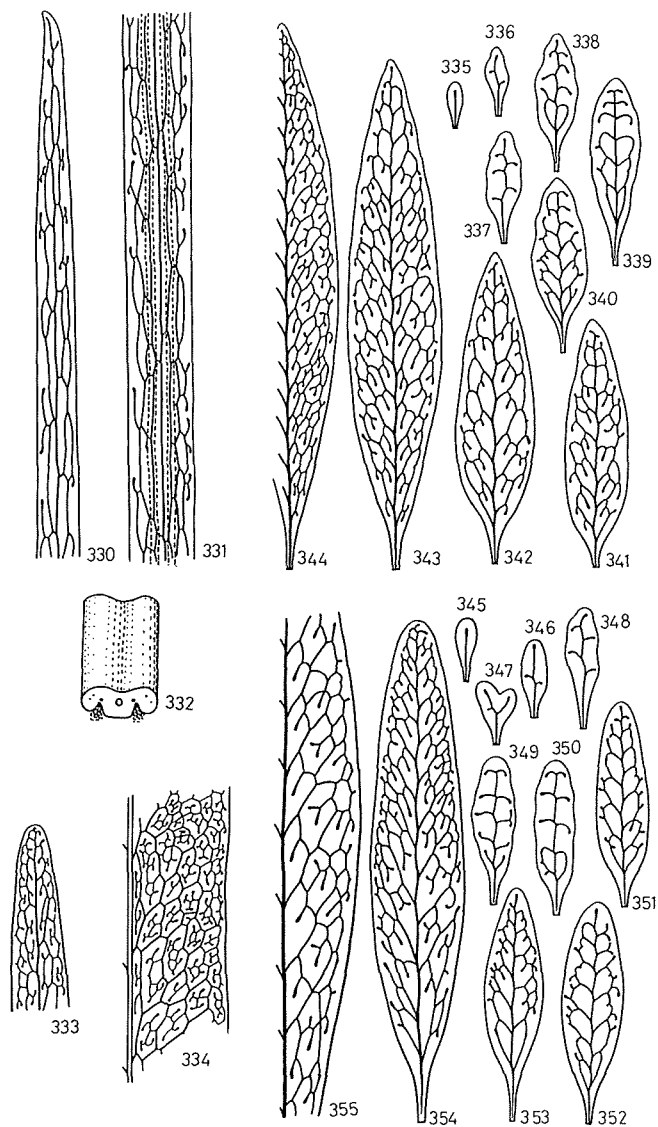
Venation of the adult leaves was observed and illustrated by BEDDOME (1883) and HOLTUM (1955); that of the juvenile leaves has not been observed.

Venation of the adult leaves of *Paragramma longifolia* (BLUME) MOORE (Figs. 333–334) is similar to that of *Lepisorus* (cf. Fig. 194) and *Microsorium* (*Phymatosorus*), as follows: the innermost (costal) areoles have recurrent included veinlets only. Outer rows of areoles have included veinlets running irregularly, which branch several times, often uniting with each other, and/or sending their branches to the outer margin of the inner rows of areoles. Areoles in the apical part of the leaf are much simpler (Fig. 333) and have only recurrent included veinlets.

### **Weatherbya COPEL.**

Venation of the adult leaves was observed and illustrated by COPELAND (1947) and HOLTUM (1955); that of the juvenile leaves has not been observed.

Venation of the adult leaves of *Weatherbya* is similar to the typical form found in *Lemmaphyllum* except for the fertile segment. My observations accord well with that of COPELAND and HOLTUM.



Figs. 330–355. 330–332: *Dryotaenium miyoshianum*, semiadult (330) and fertile leaves. 332: part of fertile leaf, showing massive structure 333–334: *Paragramma longifolia*, part of adult frond. 335–344: *Belvisia callifolia*, juvenile leaves. 345–355: *Belvisia mucronata*, juvenile leaves.

### Belvisia MIRBEL

Venation of the adult leaves of *Belvisia* was observed and illustrated by HOLTUM (1955) for *B. callifolium* (C. CHR.) COPEL.; that of the juvenile leaves was reported by MITSUTA (1981) for the same species and for *B. mucronata* (FÉE) COPEL. In these species, reticulate venation is formed (Figs. 335–355) in a way similar to that of *Lepisorus* (eg. Figs. 160–169, 170–184), and *Microsorium* (*Phymatosorus*).

In the broader-leaved species *Belvisia henryi* (HIERON. ex C. CHR.) TAGAWA, there are more than 6 rows of areoles at each side of the costa.

### Juvenile plants used in this study

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

*Platyserium bifurcatum* (Figs. 2–14), Cult. in Kyoto University Botanical garden, MITSUTA S-20, S-24. *Platyserium grande* (15–25), Cult. in Kyoto University Botanical Garden, Kosobe, MITSUTA S-387. *Polypodium vulgare* (26–32), Aomori pref. Cult. in Kyoto University Botanical Garden, MITSUTA S-249. *Polypodium plumula* (33–43), Cult. in Montréal Botanical Garden, MITSUTA S-694. *Polypodium formosanum* (44–56), Cult. in Kyoto University Botanical garden, MITSUTA S-580. *Polypodium chnoodes* (57–65), Cult. in Montréal Botanical Garden, MITSUTA S-698. *Polypodium glaucophyllum* (66–75), Cult. in Higashiyama Botanical garden, Nagoya, MITSUTA S-164, S-175. *Polypodium fallax* (76–82), Mexico (Leg. N. BASHOR), MITSUTA S-684. *Schellolepis arguta* (102–108), Taiwan, MITSUTA S-941. *Dictymia mckeei* (121–129), New Caledonia (Leg. D. W. BIERHORST), MITSUTA S-665. *Pleopeltis percussa* (131–144), Cult. in Higashiyama Botanical Garden, Nagoya, MITSUTA S-213. *Lepisorus thunbergianus* (160–169), Uji, Kyoto, MITSUTA A-61. *Lepisorus obscure-venulosus* (170–184), Taiwan, Cult. in Kyoto University Botanical Garden, MITSUTA S-251. *Lepisorus excavatus* (185–193), Madagascar, MITSUTA S-1030. *Microgramma lycopodioides* (199–214), Cult. in Higashiyama Botanical Garden, Nagoya, MITSUTA S-156, S-708. *Microgramma piloselloides* (215–224), Cult. in Higashiyama Botanical garden, Nagoya, MITSUTA S-160, S-370. *Microgramma vacciniifolia*. (225–234), Cult. in Carlos Thayas Botanical Garden, Buenos Aires, MITSUTA S-759. *Campyloneurum phyllitidis* (244–251), Cult. in Utrecht Botanische Tuinen, MITSUTA S-737. *Campyloneurum angustifolium* (252–262), Cult. in Higashiyama Botanical Garden, Nagoya, MITSUTA S-154; Cult. in Kyoto University Botanical Garden, Kosobe, MITSUTA S-247. *Phlebodium aureum* (267–277), Cult. in Higashiyama Botanical Garden, Nagoya, MITSUTA A-50. *Neocheiropteris ensata* (295–305), Ohtaki, Nara pref., MITSUTA A-154. *Lemmaphyllum microphyllum* (310–325), Mt. Sasayama, Ehime pref. MITSUTA A-75. *Belvisia callifolia* (335–344), Cult. in Higashiyama Botanical

Garden, Nagoya, MITSUTA S-166, S-379, S-385~386. *Belvisia mucronata* (345-355), New Caledonia (Leg. T. SATO), MITSUTA S-791.

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