

Studies in the Venation and Systematics of Polypodiaceae

III. Comments on generic classification of Polypodiaceae and notes on venation and systematics of Polypodiaceae

By

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Introduction for part III

Polypodiaceae in the strict sense is a family of the higher leptosporangiate ferns with about 1100 species in more than fifty genera. Generic delimitation within the family is currently based on morphology of leaves, trichomes, and soral construction. However, these characters are still insufficiently known, being mostly based on outdated and/or fragmentary information.

In parts I and II of this study, observations on the venation were made for 48 genera of Polypodiaceae and also for some from other families as to their adult leaves and/or heteroblastic series of juvenile leaves, and a characterization of the various venation types was made for the purpose of comparison and evaluation. In part III of this study, comments on the generic classification of Polypodiaceae will be presented mainly based on the observations and evaluations of the venation made in parts I and II, and the relationships between venation and systematics of the family will be discussed from the standpoint of various genera within the family. A comparison of the venation between Polypodiaceae and some other families will be made in an attempt to elucidate the systematic position of the family.

Comments on generic classification of Polypodiaceae

Platycerium

In the juvenile leaves of *Platycerium*, a simple mid-vein is more or less distinct as also observed in other genera of Polypodiaceae (Figs. 2-12, 15-23). In these stages, recurrent included veinlets seem to be predominant, although most of them originate from basal basisopic branchlets of lateral veins. In this feature, *Platycerium* differs from both *Pyrrosia* and *Microsorium*. In *Pyrrosia*, costal areoles mostly lack included veinlets, and excurrent included veinlets are predominant. In *Microsorium*, recurrent included veinlets are formed at the point of junction of both basal acroscopic and basisopic veinlets. In the later leaves of *Platycerium*,

however, the common type as seen in both *Pyrrosia* and *Microsorium* seems to be present (Figs. 12–13, 24–25).

HOSHIZAKI (1972) noted that in some species of *Platyserium* the dichotomous main-veins are united into a short mid-rib at the base of the fronds. Such a mid-rib is also observed in the juvenile leaves (Figs. 14, 25). The dichotomous branching of main veins and laminae, as suggested by JARRETT (1980), seem to be a secondary development.

The affinity of *Platyserium* to *Pyrrosia*, as noted by various authors, is mainly based on the presence of stellate hairs on laminae. Some other reasonable characters can be added here such as echinate spores of some species, coriaceous texture and xerophytic habitat, but both genera are too peculiar to be regarded as being very close to each other even with these similarities.

Polypodium and its relatives and ***Phlebodium*** (Figs. 750–790)

The venation of *Polypodium*, *Synammia*, *Schellolepis* and *Thylacopteris* is constant and uniform. Veins are free or anastomosing regularly, and form areoles usually with a single, excurrent, included veinlet in each areole. Sori are borne on either the acroscopic branch of lateral veinlets or included veinlets.

The relationship between *Polypodium* and *Synammia* was discussed by DE LA SOTA (1968), with the conclusion that the latter is better included in the former. *Synammia* is characterized by elongate sori and inequilaterally peltate scales on the rhizome. These features are shared by such species of *Polypodium* as *P. bradeorum* or *P. colysoides* (Figs. 95–96) with elongate sori, and *P. myriolepis* as to scales. *S. intermedia* (COLLA) KUNKEL of Juan Fernandez Islands has typically round sori and has the aspect of *Polypodium vulgare* in characters of scales, texture, marginal serration and decurrent base of lateral pinnae. *Synammia* may be a Southern relative of *P. vulgare* and *P. virginianum* of the Northern Hemisphere.

Schellolepis is characterized by reticulate venation, articulate lateral pinnae and peltate to ciliate paraphyses. In *S. arguta* (Fig. 118) and *S. percussa* (*Polypodium cyathoides*, Fig. 119), excurrent included veinlets sometimes branch and make loops. In the former, the basal acroscopic branch of lateral veins is sometimes forked, and forms narrower costal areoles without included veinlets, as in *Phlebodium* and *Pleopeltis*. I do not think that *Schellolepis* is a direct descendant of *Polypodium*, but its closest affinity is doubtless to *Polypodium*.

Thylacopteris is typified by deeply sunken sori. Its catadromous branching of veinlets is also unique among the *Polypodium* relatives.

Three species are recognized in *Phlebodium*: *Ph. aureum*, *Ph. decumanum* and *Ph. leucatomos*. The venation and soft, pale-castaneous scales are characteristics of this genus. Although the venation of adult leaves is complex and variable, that of juvenile leaves is comparable with that of *Polypodium*. Sori are sometimes borne at the tips of single, simple included veinlets, especially in *Ph. aureum* var. *areolatum*. Marginal notches are also present in *Phlebodium*. On the other hand, the basal acroscopic branch of lateral veins branches again and reaches the next lateral vein, resulting in the formation of narrow areoles without included veinlets. Such a character is not usual in *Polypodium*, but is found in some other species, as *P. colysoides* (Figs. 95–96), and is rather common in the juvenile leaves of *Polypodium*.

In *Phlebodium*, the receptacle of the sorus is usually borne on the tip of loop-veins which

are derived from the branches of the basal acroscopic veinlet. This is similar to the situation in *Pleopeltis* and some species of *Microgramma*.

Summarizing the above discussion, the affinity of *Phlebodium* may be to *Polypodium*, although *Phlebodium* shares some characteristics also with *Pleopeltis* and *Microgramma*.

Phlebodium*, *Microgramma*, *Pleopeltis* (s. str.), *Pyrrosia* and *Campyloneurum (Figs. 791–839)

Microgramma is separated into four to five smaller groups: *Microgramma* s. str. (*M. persicariifolia*), *Anapeltis* (*M. lycopodioides*, etc.), *Craspedaria* (*M. vacciniifolia*, etc.), *Lopholepis* (*M. piloselloides*, etc.) and the group of *M. (Polypodium) munchii*. *Microgramma* s. str. and *Anapeltis* have elaborate venation, *Craspedaria* and *Lopholepis* simple reticulate venation as *Marginaria*, and *M. munchii* has pinnatifid fronds.

Except *Microgramma munchii*, juvenile leaves of these species have the same type of venation: a row of areoles without included veinlets. In *Anapeltis*, such areoles may persist in the adult leaves, although recurrent included veinlets are often added later. In *Lopholepis* and *Craspedaria*, however, some of these areoles are usually open as excurrent included veinlets at the outer rows of areoles. *Microgramma* s. str. is typified by elongate sori, and its venation (Figs. 235–237) is similar to that of *Anapeltis* (Figs. 242–243) except for the soral commissure of the veinlets.

DE LA SOTA (1973a, b) observed that in the fertile region of *Microgramma mortoniana* DE LA SOTA, veins are often reduced and simple, resulting in venation as in *Craspedaria* and *Lopholepis*. His observation seems to support COPELAND's suggestion (1947) that the venation of *Craspedaria* and *Lopholepis* is due to simplification and does not indicate a direct affinity of this to *Polypodium*. The venation of semi-adult leaves of *M. (Anapeltis) lycopodioides* is similar to that of adult leaves of *M. (Craspedaria) vacciniifolia*, and also supports the above speculation. These variations in venation also appear in the leaves of *Phlebodium aureum*.

In *Microgramma* s. str., *Anapeltis*, *Craspedaria* and *Phlebodium*, paraphyses are simple or branched and filamentous, while those of *M. (Lopholepis) piloselloides* are clathrate and laterally fixed. Branched to stellate hairs on laminae appear in *Craspedaria* and on juvenile leaves of *Lopholepis*, the latter having inequilaterally peltate scales on adult leaves. Scales on rhizomes are peltate in *M. piloselloides*.

In *Microgramma munchii*, scales are peltate on the lamina, and inequilaterally peltate on the rhizome. Paraphyses are long filamentous or rarely branched. The included veinlets are excurrent, forming loops, the tips of which bear sori. The venation is simple in spite of its broader laminae, and no special costal areoles without included veinlets are formed. These characteristics may indicate an affinity closer to *Polypodium* than to *Microgramma*.

Another noteworthy species is *Polypodium bradeorum* (including *P. colysoides*, Figs. 95–96). Fronds are simple to pinnatisect, laminae are with stellate scales, and included veinlets are also present. This species has aspects more or less similar to *Microgramma*.

The venation of *Pleopeltis* is similar to that of *Microgramma*. Costal areoles are narrow, often without included veinlets. Recurrent veinlets within costal areoles sometimes occur between the excurrent veinlets suggesting the secondary development of recurrent included veinlets within the costal areoles as observed for *Microgramma lycopodioides*. The basal acroscopic branches of the lateral veins are sometimes included within the large outer areoles (*Pleopeltis*

macrocarpa, Figs. 156, 157). This is the common condition in *Microgramma*, *Phlebodium*, and *Polypodium*, and is never observed in *Microsorium*, *Lepisorus* and their relatives.

The venation of *Pyrrosia* is also variable. Narrow costal areoles without included veinlets are often observed in this genus. This venation pattern and the occurrence of stellate hairs on laminae and in sori (paraphyses) are like those of *Pleopeltis* (especially *P. percussa*) and/or *Microgramma* (especially *M. piloselloides*).

Laminae are glabrous in the genus *Campyloneurum*. Areoles are with excurrent included veinlets only. The basal acroscopic branches of lateral veins are usually included veinlets (*C. phyllitidis*, etc.), but these branches sometimes form narrow areoles without included veinlets in *C. angustifolium*. Paraphyses were not observed. The affinity of *Campyloneurum* is obscure, though it is conservatively related to *Polypodium*, judging from venation and leaf indument.

Pessopteris

The venation of *Pessopteris* (Figs. 265–266) is similar to that of *Pyrrosia* spp. (*P. shearerii*, *P. subfurfuracea*, etc.) and of *Microsorium*. Laminae are glabrous, though short multicellular hairs are present on rachis and costa. Sporangia are pubescent when young with short acicular hairs. Paraphyses are short, filamentous, and fugitive. These characters of venation, sporangia and leaf indument are peculiar in a member of the Polypodiaceae occurring in the New World. *Pessopteris* is an isolated genus and may be related to *Microsorium*, not to *Pleopeltis*.

Eschatogramme (Dicranoglossum)

The veins of *Eschatogramme* are anastomosing without included veinlets (Figs. 293–294). COPELAND (1947) noted that such a type of venation is found neither in *Pleopeltis* nor in *Polypodium*, though *Eschatogramme* is considered to be derived from those genera. The juvenile leaves of *Pleopeltis* (eg. *P. percussa*, Fig. 141), however, have a similar pattern of venation. Simple hair-like paraphyses were reported for *E. furcata* (WILSON, 1959).

Dictymia

The venation of *Dictymia* (Figs. 121–129) is unique in the Polypodiaceae. Areoles are principally without included veinlets. A similar venation seems to be present in some species of *Loxogramme*, but the resemblance is superficial. The absence of paraphyses, glabrous fronds and smooth to tuberculate spores do not support a relationship between the two. I prefer to place *Dictymia* in the Microsorioid group, in rather an isolated position. There are other cases in which both types of areoles without included veinlets and with recurrent ones, are known within a genus, in *Tectaria* (Dryopteridaceae) and in *Bolbitis* (Lomariopsidaceae).

***Neochheiropteris, Lepisorus* and *Microsorium* (including *Phymatodes*)** (Figs. 840–860)

A uniform pattern of venation is present in the following genera, especially in the juvenile leaves and as to marginal areoles: *Lepisorus*, *Neochheiropteris*, *Tricholepidium*, *Platygyria*, *Lemnaphyllum*, *Belvisia*, *Microsorium* (including *Phymatodes*), *Colysis*, *Dendroglossa*, *Lecanopteris*, *Weatherbya*, *Drymotaenium*, *Paragramma*, *Diblemma*, *Leptochilus* and *Paraleptochilus*. They are all Paleotropical, and are related to the *Microsorium* and/or *Lepisorus* complex in various characters (COLEPAND, 1947; HOLTUM, 1955). There is no New World genus with exactly the same pattern

of venation, although similar venation is present in *Pessopteris*, *Solanopteris brunei* (WAGNER, 1972) and *Polypodium* (*Microgramma*?) *megalophyllum* (Fig. 198). A species of *Microgramma* (*M. lycopodioides*) may be added to them, but observation of the ontogeny of the venation of this species (Figs. 199–214) suggests that such venation has been derived along a different evolutionary course. *Pessopteris* and *Solanopteris* are small genera, and endemic to the American tropics. In *Solanopteris brunei*, the areoles along the main-vein often lack included veinlets (WAGNER, l.c. Fig. 3D), and show a pattern similar to *Microgramma*.

In *Microsorium* s. str., the innermost areoles are usually close to the costae, and outer large areoles are disposed in a more or less regular arrangement. This is not generally the case in *Phymatodes*, but does not seem to show an essential difference for a genus as its juvenile leaves have the same type of venation.

Neocheiropteris, *Lepisorus* and *Microsorium* include many species and/or are widely distributed, and share common characters of clathrate scales, venation type and spore features.

Lepisorus* and *Pleopeltis

The venation of juvenile leaves of *Lepisorus* is different from that of *Pleopeltis*. In the former, lateral veins form areoles with recurrent included veinlets only in the juvenile leaves, while in the latter excurrent included veinlets are formed in marginal areoles beyond the narrow areoles along the costa. These narrow areoles are observed in both genera, but the areoles have catadromous branches of lateral veins in the former, a characteristic feature of *Lepisorus* and the *Microsorium* group. In *Pleopeltis*, however, the areoles are formed by anadromous branching in the juvenile leaves. Catadromous branching is also found occasionally in the adult leaves of some *Pleopeltis* species (Figs. 158–159), but even then excurrent free included veinlets are present in the narrow areoles. In *Campyloneurum angustifolium*, lateral vein branchlets are anadromous in the juvenile leaves (Figs. 260–262), but catadromous in adult leaves (264). Excurrent free included veinlets are also present. This catadromous branching seems to be a result of the loss of some veinlets.

The Neotropical genera *Phlebodium*, *Microgramma*, *Pleopeltis*, and some species of *Polypodium* have similar features in the venation patterns of the juvenile leaves. These observations accord well with those of DE LA SOTA (1973b) except for *Phlebodium* which he did not discuss.

The resemblance between *Lepisorus* and *Pleopeltis* seems to be superficial. *Lepisorus* is Microsorioid, while *Pleopeltis* is apparently related to *Polypodium*, *Microgramma* and *Phlebodium*.

Lemmaphyllum*, *Drymotaenium*, *Weatherbya*, *Belvisia*, *Paragramma* and *Tricholepidium

The venation of these genera is similar to each other. Peltate paraphyses and tuberoso to verrucose spore surfaces are also common features of these genera except that *Drymotaenium* has nearly smooth spores. *Lemmaphyllum* and *Belvisia* are usually considered relatives of *Lepisorus*. The venation of *Drymotaenium* (Figs. 330–331) is rather simple, the result of simplification of the linear fronds.

Trilete spores were observed in *Weatherbya accedens* (KREMP and KAWASAKI, 1972). Materials I examined agree with theirs. *Weatherbya* is also different from *Lemmaphyllum* in the fimbriate margins of rhizome scales, thinner texture of frond and round sori.

Paragramma has a glabrous lamina and a variety of paraphyses ranging from simple hairs to typically peltate scales and differs from *Lepisorus* in these features. *Tricholepidium* is different from *Lepisorus* and *Neocheiropteris* in the texture of fronds and in having bristle-bearing scales on rhizome.

Diblemma

The venation of *Diblemma* is similar to that of *Microsorium*. Although the linear coenosori are at the margins of the fronds, small, round to elongate sori are sometimes present on the lamina close to costae. *Diblemma* may be related to *Microsorium tenuilore* (J. SMITH) COPEL., agreeing in characters of frond shape, venation of sterile fronds as well as scales on rhizome.

Lecanopteris* and *Solanopteris

The venation of juvenile leaves of *Lecanopteris carnosa* (Figs. 535–544) is similar to that of *Microsorium* and *Lepisorus*. Branchlets of lateral veins are in a catadromous arrangement, a characteristic of the Microsorioids.

Juvenile leaves of *Solanopteris* were not available for this study. Venation of adult leaves includes both anadromous and catadromous branching in even a single leaf (WAGNER, 1972, Fig. 3–A, C, D), though mostly anadromous in fertile leaves (Fig. 3–E, F). In *Microgramma*, lateral branches are anadromous in juvenile leaves. In the adult leaves of some species of *Microgramma*, however, the branching is both anadromous and catadromous or only catadromous (*M. lycopodioides*, Figs. 212–214, 242–243).

Lecanopteris*, *Lepisorus* and *Microsorium

These three genera are similar to each other in venation and soral characteristics (except paraphyses). *Lecanopteris* and *Microsorium* have short filamentous paraphyses and not peltate ones. Rhizome scales of *Lecanopteris* are not similar to *Microsorium* but to *Lepisorus*. In juvenile plants of *Lecanopteris carnosa*, simple to branched glandular hairs are present on the lamina (Fig. 550) and the rhizome (Fig. 547). In mature plants, these glandular hairs become the scales, at first basally attached (Fig. 548), and then inequilaterally to typically peltate and clathrate (Fig. 549). The difference in rhizome scales between *Microsorium* and *Lecanopteris* seems to be minor. *Lecanopteris* should better be related to *Microsorium* (*Phymatodes*) than to *Lepisorus*.

Pyrrosia*, *Drymoglossum* and *Saxiglossum

The venation of *Pyrrosia* is rather variable. Almost all the species have reticulate venation with excurrent included veinlets. In the species with smaller leaves or narrow laminae, included veinlets are all excurrent, and costal areoles lack included veinlets (*P. adnascens*, Figs. 368–370; *P. nummularifolia*, 372; *P. linearifolia*, 373–375; etc.). In the species with larger leaves, recurrent included veinlets sometimes appear (*P. lingua*, Fig. 366; *P. shearerii*, 376–377). The venation of the former is often referred to as Campyloneuroid, and the latter as Microsorioid (NAYAR and CHANDRA, 1967). In the former (*P. adnascens*, etc.), the branchlets of the lateral veins are catadromous and costal areoles lack included veinlets. In the latter, excurrent free included veinlets, which do not originate from the hamate branches of recurrent veinlets are

sometimes present. This character is not found in the *Microsorium* group. The venation of *P. lingua* was referred to as irregularly Microsorioid (NAYAR and CHANDRA, l.c.), but as seen in the juvenile leaves (Figs. 364–365), the veins are similar to those of the smaller species with typical excurrent included veinlets. The Microsorioid appearance of the venation of *Pyrrisia* seems to result from variation caused by expansion in breadth of the lamina.

The venation of *Drymoglossum piloselloides* (Figs. 378–380) is quite different from that of *D. fallax*. The former has a typically Microsorioid venation. Excurrent included veinlets are sometimes distinct, but seem to originate from the hamate branches of recurrent included veinlets as in the leaves of *Lemmaphyllum*. NAYAR (1957) reported that the leaves of *Pyrrisia* passed through the stages represented by mature leaves of *Drymoglossum* in venation. He did not mention, however, in which species he made the observation, nor did he give any illustrations of the successive development of venation in the juvenile leaves. Spores of *D. piloselloides* are echinate, not the same as those of *Pyrrisia* (smooth to verrucose) nor of *Microsorium* (smooth, tuberoso or verrucose). Although the presence of stellate hairs on laminae seems to indicate that *Drymoglossum* has affinity to *Pyrrisia*, venation and spore characters of *D. piloselloides* are peculiar when compared with *Pyrrisia* species.

The venation of *Saxiglossum* is very similar to that of *Pyrrisia*, especially *P. linearifolia*. It is recognized as a derivative of *Pyrrisia*, or is even reduced to the latter.

Microsorium*, *Drynarioid* ferns and *Crypsinus (Figs. 840–896)

In the juvenile leaves of Drynarioid ferns, both excurrent and recurrent free included veinlets appear even within a single leaf, and branchlets of the lateral veins are catadromous and/or anadromous both within a single leaf. The costal areoles sometimes include excurrent free veinlets, sometimes recurrent ones only, or may lack any included veinlets. Excurrent included veinlets are predominant in *Drynaria propinqua* (Figs. 506–509). Although the variable venation types of Drynarioid ferns appear to be similar to those of *Microsorium*, the relationship is not supported by the venation of the juvenile leaves which is different between Drynarioid ferns and *Microsorium*. *M. linguiforme* and *M. musifolium* are sometimes regarded as species linking *Microsorium* and Drynarioid ferns, but the venation of these two species is typical of *Microsorium*. Long, soft, multicellular hairs appear in *Holostachyum*, in juvenile leaves of *Merinthosorus* (NAYAR, 1965), *Photinopteris*, *Drynaria propinqua*, *Dyrostachyum splendens*, *Aglaomorpha meyeniana* and *A. pilosa*. Short hairs are observed in *Drynariopsis heraclea*. These multicellular hairs are absent in *Microsorium* and its direct relatives, but are found in some species of *Polypodium*. Juvenile leaves of the Drynarioid ferns often have marginal notching which is common in *Polypodium* and *Crypsinus*.

The venation of *Crypsinus* is also variable; branching patterns of lateral veinlets are also variable. In this genus, however, costal areoles usually have recurrent veinlets only. In the outer rows of areoles, excurrent included veinlets are predominant as in *C. pyrrolifolius* (fig. 572). The variation of the venation patterns in *Crypsinus* is noted in the description of the venation in the preceding chapter.

In *Crypsinus hastatus*, the venation of the juvenile leaves is similar to that of *Microsorium*, but this is an exceptional case in this genus. In *C. albido-squamatus* recurrent included veinlets are wholly lacking in the outer rows of areoles (Figs. 577–581), and are present between the

excurrent ones in the costal areoles. Marginal notching is also observed in many species of this genus.

Some austral species of *Microsorium*, *M. scandens*, *M. diversifolium* and *M. vieillardii*, are sometimes regarded as relatives of *Crypsinus*. Their venation is simple with only a few rows of areoles along the costa, but otherwise indetical to that typical for *Microsorium*, as also are the juvenile leaves of *M. vieillardii* (Figs. 393–399). Spores of these species do not have sculpturing characteristic of *Crypsinus*.

Summarizing the above discussion, the Drynarioid ferns and *Crypsinus* are distinct from *Microsorium* and its direct derivatives. The Drynarioid ferns may better be related to *Polypodium*, while *Crypsinus* is probably nearer to *Microsorium*. The venation of the Drynarioid ferns is far more complex than that of *Polypodium*, but parallel examples are found in such cases as *Steg-nogramma* (IWATSUKI, 1962, 1963) and *Bolbitis* (HENNIPMAN, 1977).

Pycnoloma*, *Grammatopteridium*, *Holcosorus*, *Selliguea* and *Arthromeris

These genera are separated from *Crypsinus* by such characters as having distinctly dimorphic fronds, thick texture of lamina, narrowly linear fronds, elongate coenosori and articulations at the base of lateral pinnae.

In *Pycnoloma* (Figs. 583–585), included veinlets are mostly excurrent and marginal notching is observed in some species. *Pycnoloma* may be a direct derivative of *Crypsinus* through such a species as *C. enervis* (Figs. 566–568).

The venation of *Grammatopteridium costulatum* (Figs. 586–587) is the same as that of *Crypsinus* and different from that of *Microsorium*.

The venation of *Holcosorus* (Figs. 588–589) is extremely simple for these genera. Areoles are mostly without included veinlets, a very unusual case in *Crypsinus* derivatives. This type of simple venation is seen in the juvenile leaves of *Crypsinus* (Figs. 557–558), and the venation of *Holcosorus* may be recognized as a result of simplification of frond construction. Vestigial marginal notches are present at frond apices.

Selliguea is characterized by elongate coenosori and rigid coriaceous texture of the frond. The venation of *S. feei* and *S. heterocarpa* is identical to that of *Crypsinus*, and *S. lima* seems to be intermediate between *Selliguea* and *Crypsinus* in both soral characters and texture of lamina (Figs. 590–604).

Arthromeris is diagnosed by imparipinnate fronds and the presence of articulate lateral pinnae. Excurrent free included veinlets, which do not originate from hamate branches of recurrent included veinlets are commonly observed in the genus (Figs. 605–607). The genus has similarities to *Microsorium cuspidatum* of also with imparipinnate fronds, but the venation of the latter is typical of *Microsorium* and articulation is absent. On the other hand, *Arthromeris* has similarities to *Polypodium* and/or *Schellolepis* in venation, soral characteristics and presence of marginal serrations. *Arthromeris* does not seem to be a direct descendant of *Crypsinus*, but is related to *Crypsinus*.

Polypodiopteris

The venation of *Polypodiopteris proavita* is simple as was illustrated by COPELAND (1947, Pl. X). In broader pinnae with undulate margins, the veins are more complex, with two or

three rows of areoles on each side of the costae (Fig. 608). The venation of *Polypodiopteris* seems also to be a result of simplification of frond construction. *Polypodiopteris* has pectinate fronds, but has no direct affinity to *Polypodium*, as the former has narrow areoles without included veinlets along the costa. Most areoles in *Polypodiopteris* lack included veinlets, but the same pattern is observed in *Holcosorus*, which is a direct derivative of *Crypsinus*.

***Loxogramme* and *Anarthropteris* (Figs. 905–934)**

The systematic position of *Loxogramme* was discussed by KONTA (1978) with the conclusion that it belongs in Polypodiaceae s. str. Although he suggested an affinity of *Loxogramme* to Microsoroid ferns, especially to *Colysis*, its position in this family is still not clear. Hydrathodes seem to have no connection to the tips of included veinlets in this genus. This character is also present in *Dictymia*, *Anarthropteris* and several species in other genera, and also in Vittariaceae.

The venation of *Loxogramme* is similar to that of the Drynarioid ferns in the species with large and broad fronds, or is simple Sagenioid in the smaller fronds. The latter type of venation is also found in *Dictymia* and *Anarthropteris*. The ontogeny of the former type of venation is distinct from that of *Microsorium* and *Colysis*. The resemblance in venation between *Loxogramme* and *Colysis*, both with elongated sori, seems to be superficial rather than phyletic, and KONTA's conclusion cannot be accepted, at least in this respect.

Pleurosoriopsis

The systematic position of *Pleurosoriopsis* has been discussed in recent years by MASUYAMA (1975), NAYAR (1977), and KURITA and IKEBE (1977). NAYAR noted the resemblance between *Pleurosoriopsis* and some genera of Polypodiaceae, especially *Christiopteris*, in characters of spores, and sequence of the cell divisions of the prothallus during germination and development. KURITA and IKEBE carefully studied the characters of sporophytes, especially non-jointed stipes and the trichomes on surface of rhizome and scales, as well as at the base of the stipes. Based on these specialized characters, they proposed to recognize a monotypic Pleurosoriopsidaceae.

Trichome-bearing scales are known in some genera of the Polypodiaceae; a typical one is *Tricholepidium*, or the *Microsorium normale* group. In *T. normale*, bristle-like hairs are found on the abaxial surface of rhizome-scales, and consist of one or two cells. The scales are similar to those of *Pleurosoriopsis* in structure and ferruginous color. In *Tricholepidium*, however, these trichomes are neither on the rhizome nor on stipes. Stipes have no distinct abscission layer in *Pleurosoriopsis*. The lack of a jointed stipe is quite unusual in Polypodiaceae, but known in smaller plants of *Loxogramme* (KONTA, 1974) and some of the Drynarioid ferns.

The venation of *Pleurosoriopsis* (Fig. 636) is so-called Caenopteroid, one of the commonest types among the Leptosporangiate ferns, and is also found in *Polypodium lindenianum* (Figs. 87–88) and *P. fallax* (80–82).

Sporophytes of *Pleurosoriopsis* begin to develop their fronds in early autumn and grow in winter, shedding their fronds during the next midsummer, though it grows in cooler areas of northern East Asia. The same ecology is also known for some species of Polypodiaceae, as *Polypodium fauriei* and *P. niponicum*, and quite unusual in the other families.

Summarizing the discussion above, I prefer to place *Pleurosoriopsis* in Polypodiaceae. The special trichomes on rhizome and stipes are, however, peculiar even in this family.

Notes on venation and systmatics of Polypodiaceae

The venation of Grammitidaceae is mostly free and more or less simple. The venation of some species of *Ctenopteris* (Figs. 637–644) is comparable with that of *Polypodium*: *C. tenuisecta* (637) with *P. fallax* (82) and *P. lindenianum* (87–88), *C. brevivenosa* (638–639) with the juvenile leaves of *P. plumula* (51–45), and *C. sp.* (641–644) with *P. formosanum* (56, 84) or with the juvenile leaves of *P. chnoodes* (64–65). The more complex reticulation seen in *Glyphotaenium spongiosum* (640) is characteristic in having, though mostly casual, narrow areoles without included veinlets along the costa. In distal parts of the frond, the veins are free or reticulate in a way similar to *Polypodium*.

Veins are all free in Gleicheniaceae. In each segments, the branches of lateral veinlets diverge at a broad angle to each other, especially in *Dicranopteris* (646). This type of venation is not present in the adult leaves of Polypodiaceae.

In *Phanerosorus* (Figs. 648–650) of Matoniaceae, reticulation of the veinlets is observed in both sterile and fertile segments, very infrequently in the former and rather commonly in the latter. The venation of this genus is comparable with that of *Polypodium* and of the juvenile leaves of *Phlebodium* and others. Reticulation of the veins is rather specialized in *Matonia* (647). The presence of narrow areoles along the main-vein might be derived in a way similar to that observed in *Phanerosorus*. Sori are borne on the plexus of the veinlets, also observed, though in simpler form, in some genera of Polypodiaceae, such as *Selliguea* and *Microgramma*. The pedate frond of *Matonia* is also known in Polypodiaceae, as in *Neocheiropteris* and *Colysis*, but is not identical to that of *Dipteris* as was pointed out by DE LA SOTA (1963).

The reticulate venation of Dipteridaceae (Figs. 651–653) appears similar to that of *Christiopteris*, *Microsorium* and its relatives. The juvenile leaves of *Dipteris conjugata* described by WAGNER (1952) show that main veins are always dichotomous and included veinlets are not always 'recurrent' (or towards the main-veins) in this genus. In this respect, the venation of *Dipteris* is not identical to that of *Microsorium* and its relatives, but is similar to some juvenile leaves of *Cheiropleuria*, as will be discussed below.

In juvenile leaves of *Cheiropleuria*, the main-vein is sometimes dichotomous in the first leaves but is simple in some leaves (Figs. 654–655, 657–658, 660–662). In the latter case, included veinlets are formed in the same way as in *Microsorium* and its relatives. The main-vein becomes dichotomous in the larger or adult leaves. The venation of *Cheiropleuria* is in general well comparable with or even identical with that of Polypodiaceae.

Comparison of the venation between Polypodiaceae and other families

Dryopteridaceae subfam. Tectarioideae (figs. 937–997)

The venation pattern and its ontogenetical development are seemingly similar between Tectarioideae and Polypodiaceae, though in some features the venation is characteristic for each.

In *Lastreopsis sp.*, fronds are deeply dissected from the very young stages, similar to the development of *Polypodium fallax* and probably also of *P. lindenianum*. In species of *Ctenitis* and of *Tectaria* with dissected fronds, ontogenetic development of the venation is similar to that of

Polypodium, though the basal basiscopic pinnules of the lowermost pinnae are often well developed in the former two genera.

In species of *Hemigramma*, *Quercifilix* and *Tectaria* with simple or slightly dissected fronds, the juvenile leaves have entire margins and anastomosis of the lateral veinlets occurs first without included veinlets, later with both or either recurrent and/or excurrent included veinlets. This type of development is well represented in *Drynaria*, *Crypsinus* and *Microsorium*. In the case of *Tectaria decurrens* and *Hemigramma decurrens*, the included veinlets are mostly recurrent, and the venation is identical with that of *Microsorium* and its relatives, while in *T. barberi* included veinlets are all excurrent and the venation as a whole is identical with that of some species of *Crypsinus*, *Pyrrosia* and *Phlebodium*. The types of venation observed within the genus *Tectaria* indicate that the various patterns of venation observed in Polypodiaceae may not directly show differences in phylogeny, and the relationships of each genus are better understood by utilizing numerous characteristics of each taxon.

In *Pleocnemia*, anastomosis of veins occurs in the same way as that observed in *Pteris*. A similar case is observed in *Tectaria gemmifera*, though the margins of lobes are less dissected than in the case of *Pleocnemia*. Areoles of these species are all without included veinlets. This type of venation is not observed in any species of Polypodiaceae.

Lomariopsidaceae

Venation patterns of *Bolbitis* were described and discussed in detail by HENNIPMAN (1977). In this genus, venation of the *Microsorium*-type is observed in several species, such as *B. hemionitis* (MAXON) CHING, *B. oligarchica* (BAKER) HENNIPMAN, *B. hastata* (FOURN.) HENNIPMAN, *B. nicotianifolia* (SW.) ALSTON, and *B. semipinnatifida* (FÉE) ALSTON. They are mostly species of the American and/or African tropics. According to the illustrations of HENNIPMAN (l.c.), the juvenile leaves of the latter three species have venation similar to that of *Microsorium*. Several other species are comparable with members of Polypodiaceae in venation:

Bolbitis bipinnatifida (J. SM.) K. IWATS. with *Campyloneurum*

B. virens (H. & G.) SCHOTT, *B. costata* (PRESL) CHING and *B. subcrenata* (H. & G.) CHING, with *Pyrrosia* and *Phlebodium*

B. fluviatilis (HOOK.) CHING, with *Anarthropteris*, *Dictymia* and *Loxogramme*

B. appendiculata (WILLD.) K. IWATS. with *Polypodium* (sterile)

B. heteroclita f. (*Edanyoa difformis* COPEL.) with *Polypodium fallax* and *P. lindenianum*.

Compared with Polypodiaceae, the venation of *Bolbitis* is distinct in the absence of excurrent included veinlets within the costal areoles. The reticulate venation of the *Polypodium* and *Goniophlebium* type, thus, is not found in this genus. Except for this difference, various venation patterns found in Polypodiaceae are also represented in *Bolbitis*.

The developmental process in formation of Drynarioid venation

The most complex and elaborate venation in Polypodiaceae, or in the ferns in general, is so-called Venatio Drynarioideae (LUERSEN, 1889). In this type of venation, costal-nerved and/or lateral veins are thick and straight, the secondary veins are distinct and rather straight,

and within the areoles are many smaller areoles. These smaller areoles often lack included veinlets.

Based on the observations made in this study, two different types are recognized within Drynarioid venation, especially in their ontogeny.

I. *Drynaria* type (Drynarioid venation s. str.)

Included veinlets are irregular in their direction in the juvenile leaves.

Drynaria and its direct relatives; some species of *Crypsinus* belong to this type; some of *Loxogramme* (*L. forbesii*, *L. nidiformis*) may also be added here.

II. *Microsorium* type

Directly derived from Microsorioid (Anaxetioid) venation; Included veinlets are recurrent only in the juvenile leaves.

Some species of *Microsorium* (*M. membranaceum*, *M. linguiforme*, *M. commutatum* (BL.) COPEL.); the large leaved species of *Neocheiropteris* and *Colysis*.

These two types are distinct in their ontogeny, but hardly distinguishable from each other in the adult leaves. The characteristic of the included veinlets in marginal areoles is often helpful in distinguishing different types; the included veinlets are quite irregular in their orientation in the former, while typically recurrent in the latter.

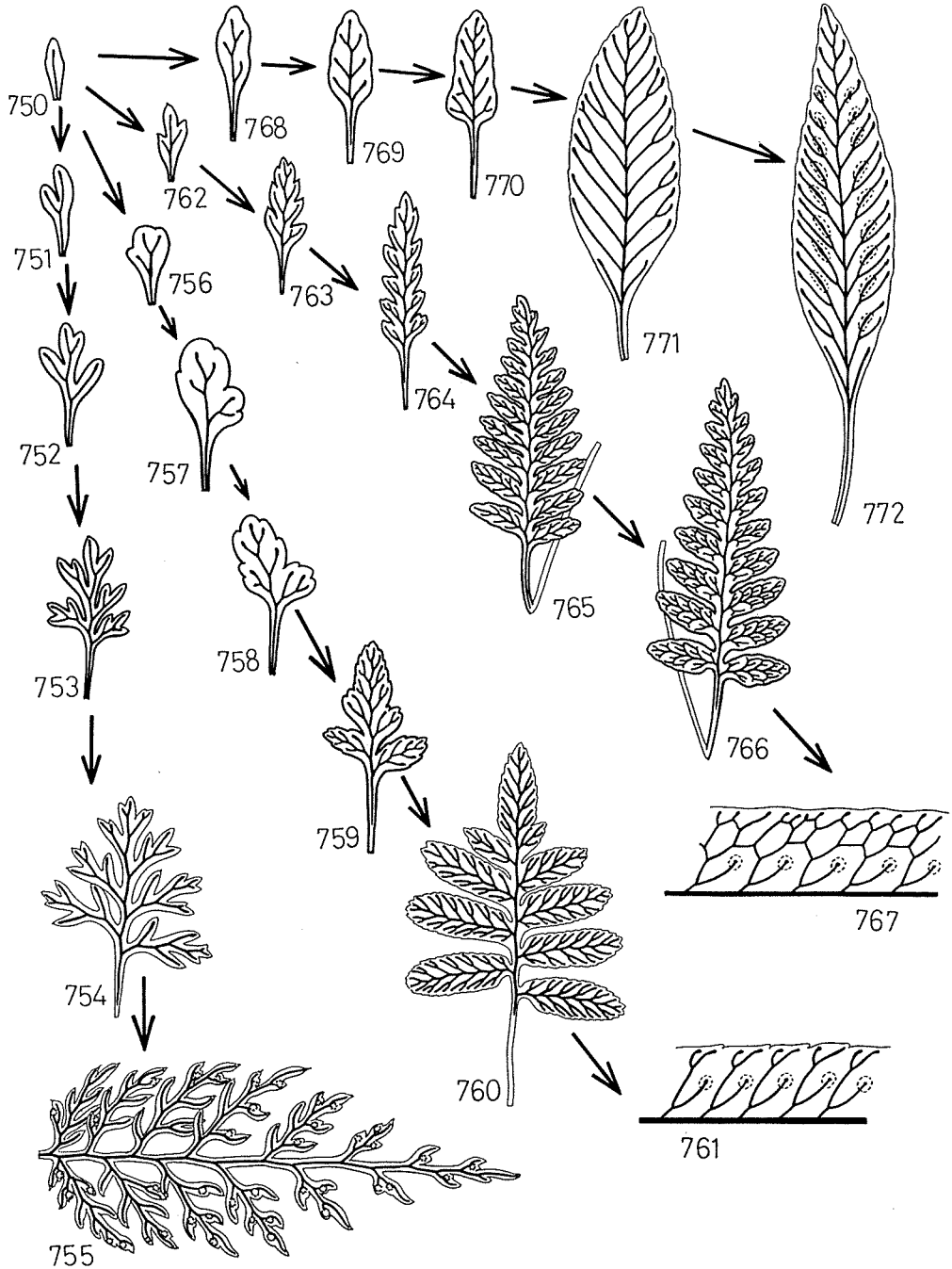
The venation of *Pyrrosia* is sometimes complex, and areoles are ontogenetically often with excurrent included veinlets only. Even the best developed venation of *Pyrrosia* is, however, usually too simple to be called Drynarioid.

Marginal union of the veins as seen in Pteridaceae, Aspleniaceae (*Neottopteris*), Vittariaceae (*Vittaria*) and Athyriaceae (*Hemidictyum*) is not found in Polypodiaceae. The venation of *Eschatogramme* (Figs. 293–294) and *Loxogramme subselliguea* (Figs. 633–634) appears similar, but both are merely the result of reduction to a narrow lamina which does not permit much reticulation.

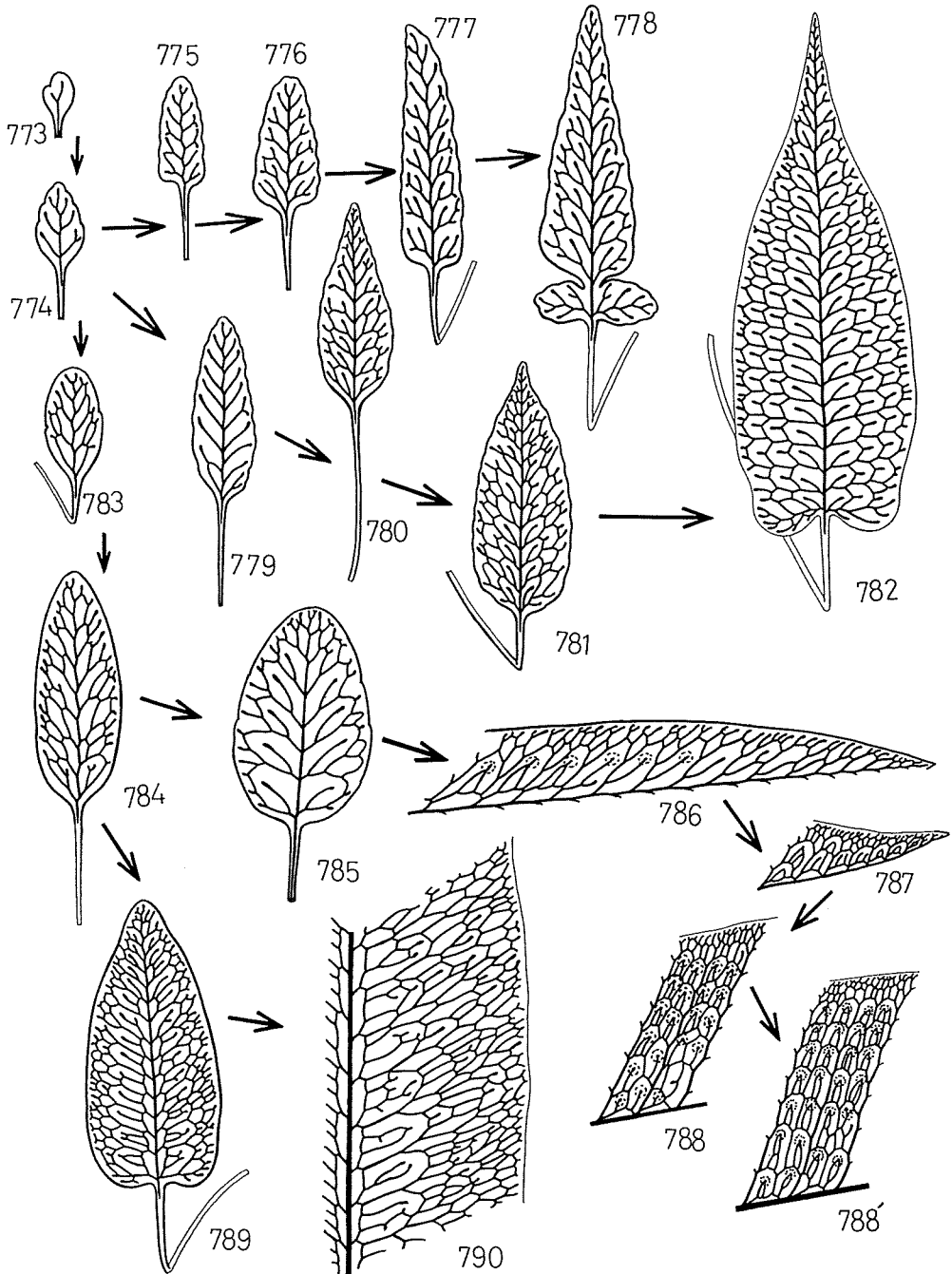
In almost all genera of the Polypodiaceae, the tips of the veinlets are swollen. Such a swelling is, however, totally lacking in the genera *Loxogramme*, *Anarthropteris* and *Dictymia*.

It is still impossible to make any conclusions as to the relationship between early Polypodiaceae and early Dipteroids or Gleichenioids. Information about the juvenile leaves is still insufficient for *Dipteris*. The resemblance of the venation of *Dipteris* and *Microsorium* may be deceiving. Venation of the *Polypodium* type appears in *Phanerosorus* (Matoniaceae). Such a venation, however, could also evolve independently as it has in some genera of Dryopteridaceae such as *Cyrtomium* (MITSUTA, 1977), *Phanerophlebia*, or in the free venation of *Cyclopeltis*.

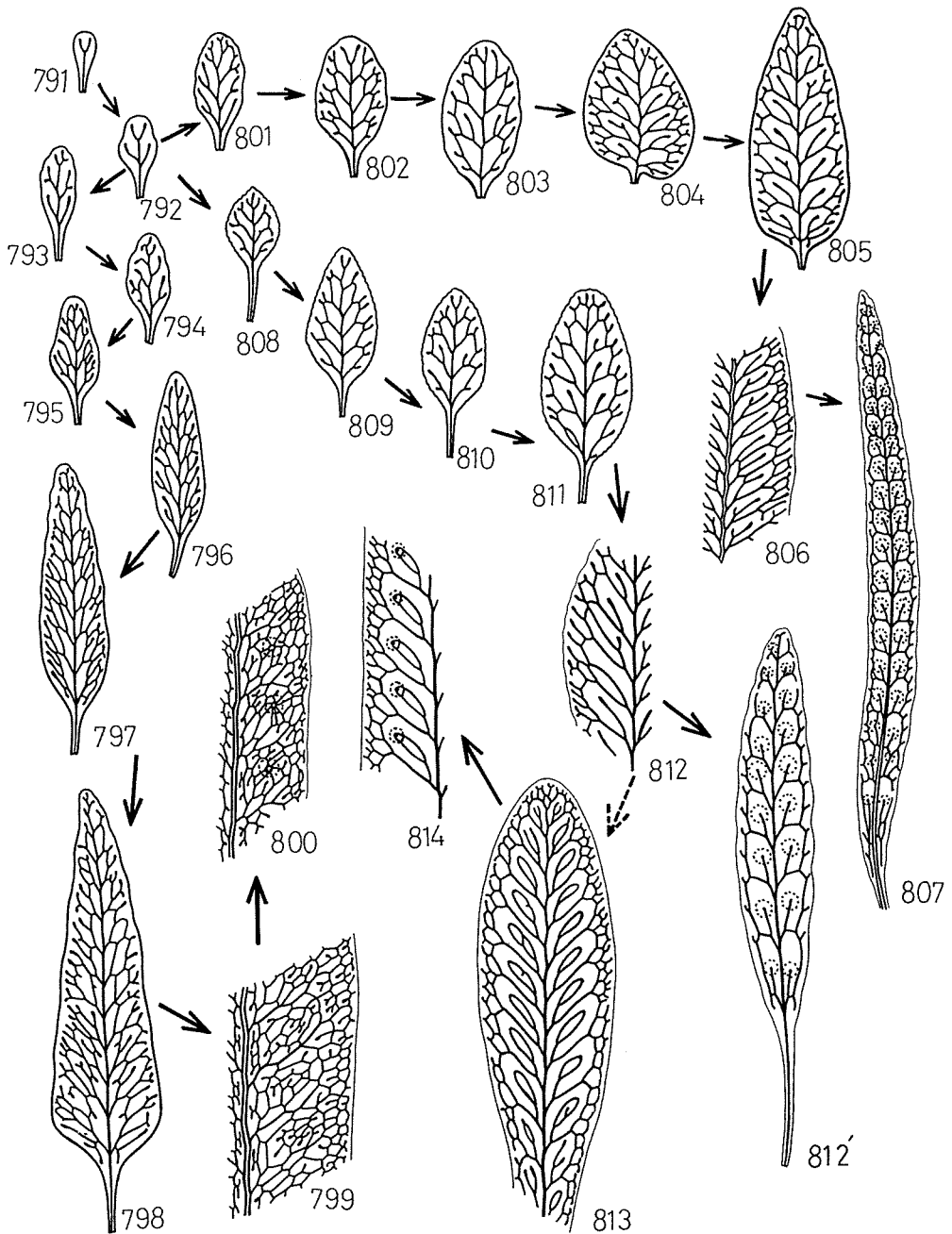
The included veinlets of irregular direction seen in Drynarioid and other ferns seem to be intermediate between the *Microsorium* and *Polypodium* type, and require further studies.



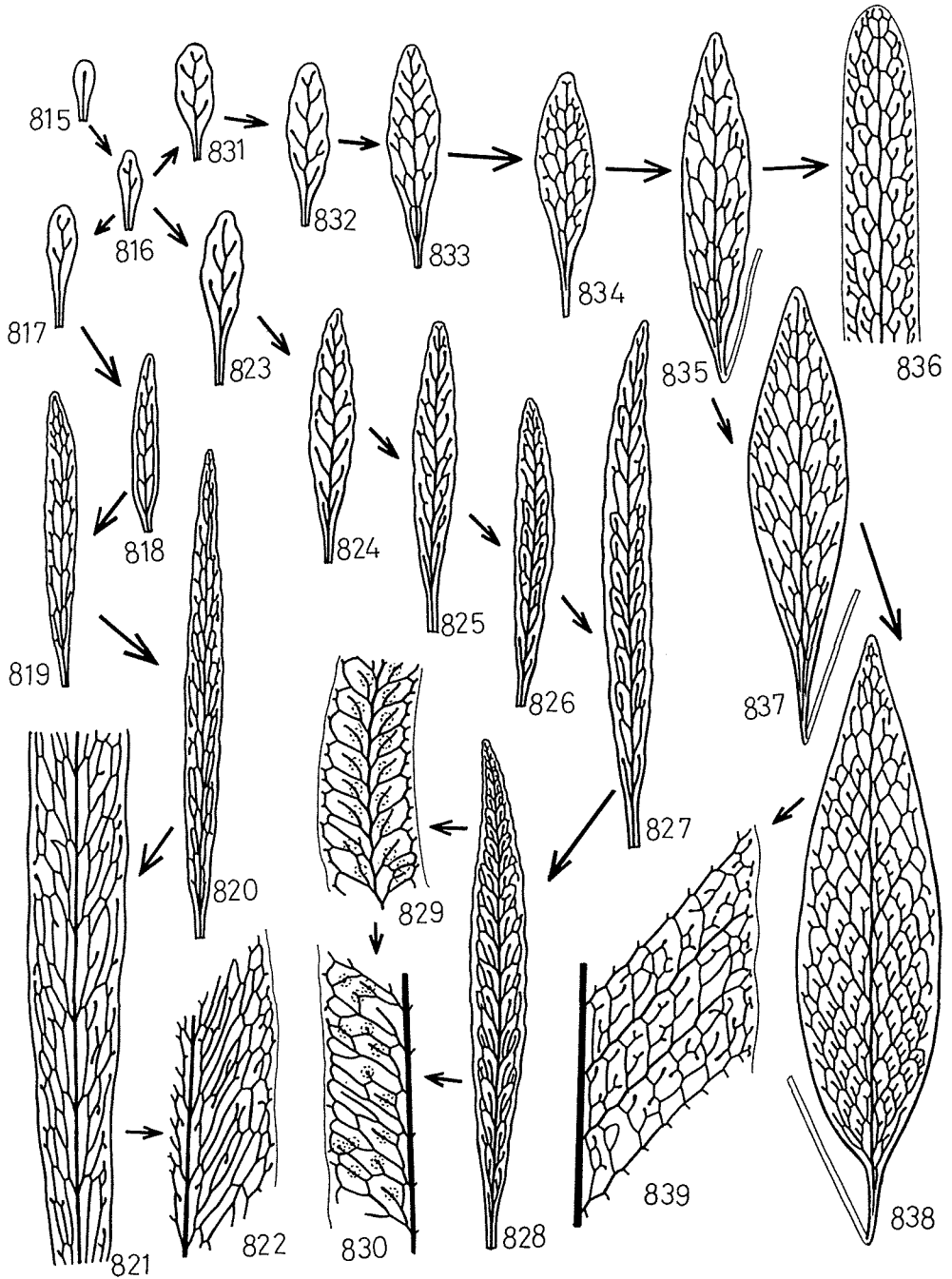
Figs. 750-772. Four types of serial development of venation in *Polypodium* s. str. 750-755: *Polypodium fallax* type (754: *P. fallax*. 755: *P. lindianum*). 750, 756-761: *P. vulgare* type (760-761: *P. vulgare*). 750, 762-767: *P. formosanum* type (766-767: *P. formosanum*). 750, 768-772: *P. sp.* type, (771-772: *P. sp.*).



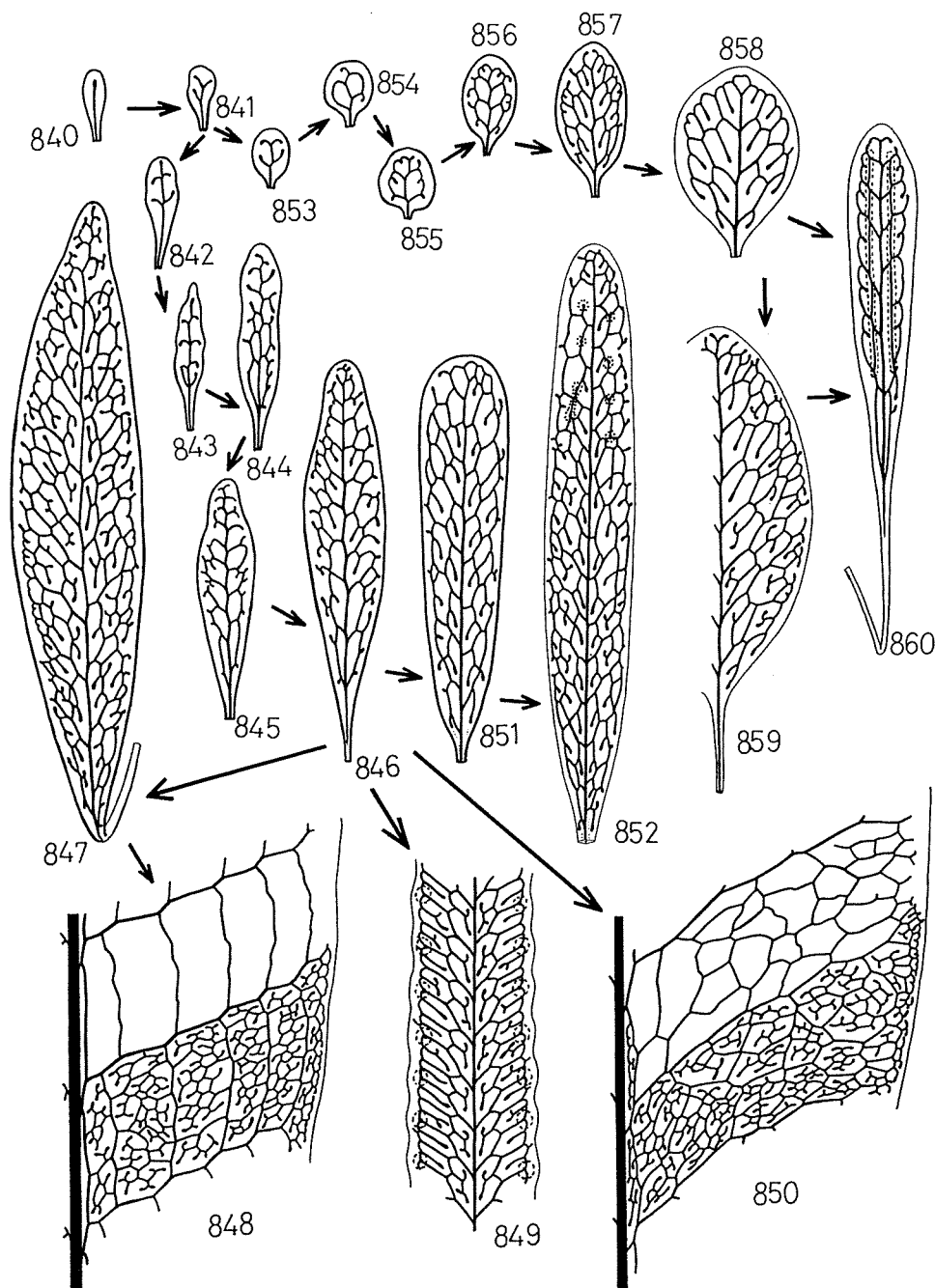
Figs. 773-790. Venation of *Polypodium* and *Phlebodium*. 773-778: *Polypodium chnoodes*. 773, 774, 779-782: *Polypodium glaucophyllum*. 773, 774, 783-788: *Phlebodium aureum* var. *areolatum* (786) and *Ph. decumanum* (787-788). 784-790: *Phlebodium aureum* var. *aureum*.



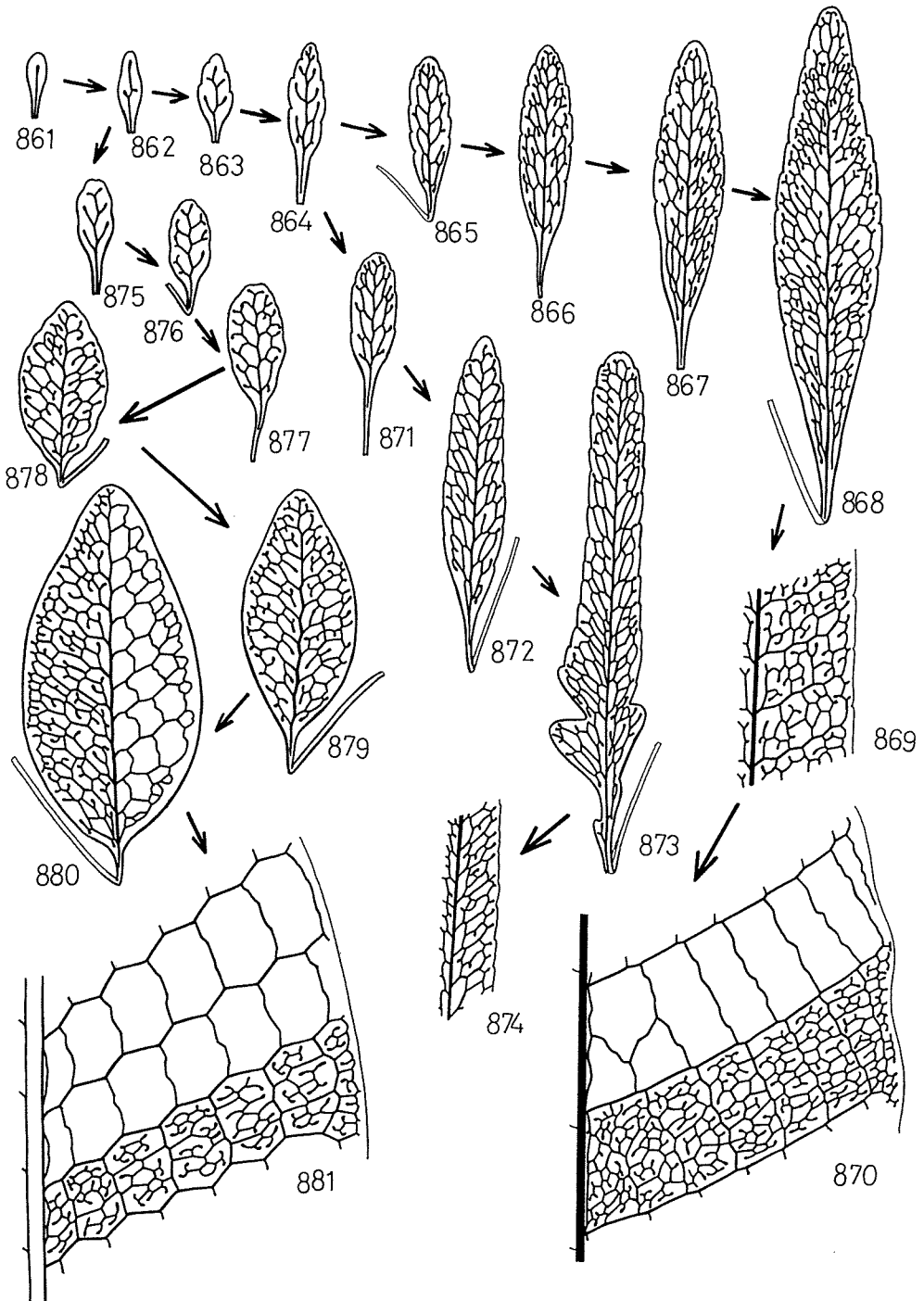
Figs. 791-814. Venation of *Microgramma* s. lato. 791-800: *Microgramma* (*Anapeltis*) *lycopodioides*, and probably *M. persicariifolia*. 791, 792, 801-807: *M. (Craspedaria) vacciniifolia*. 791, 792, 808-812: *M. (Lopholepis) piloselloides*. 812(-)813-814: *Polypodium (Microgramma?) munchii*.



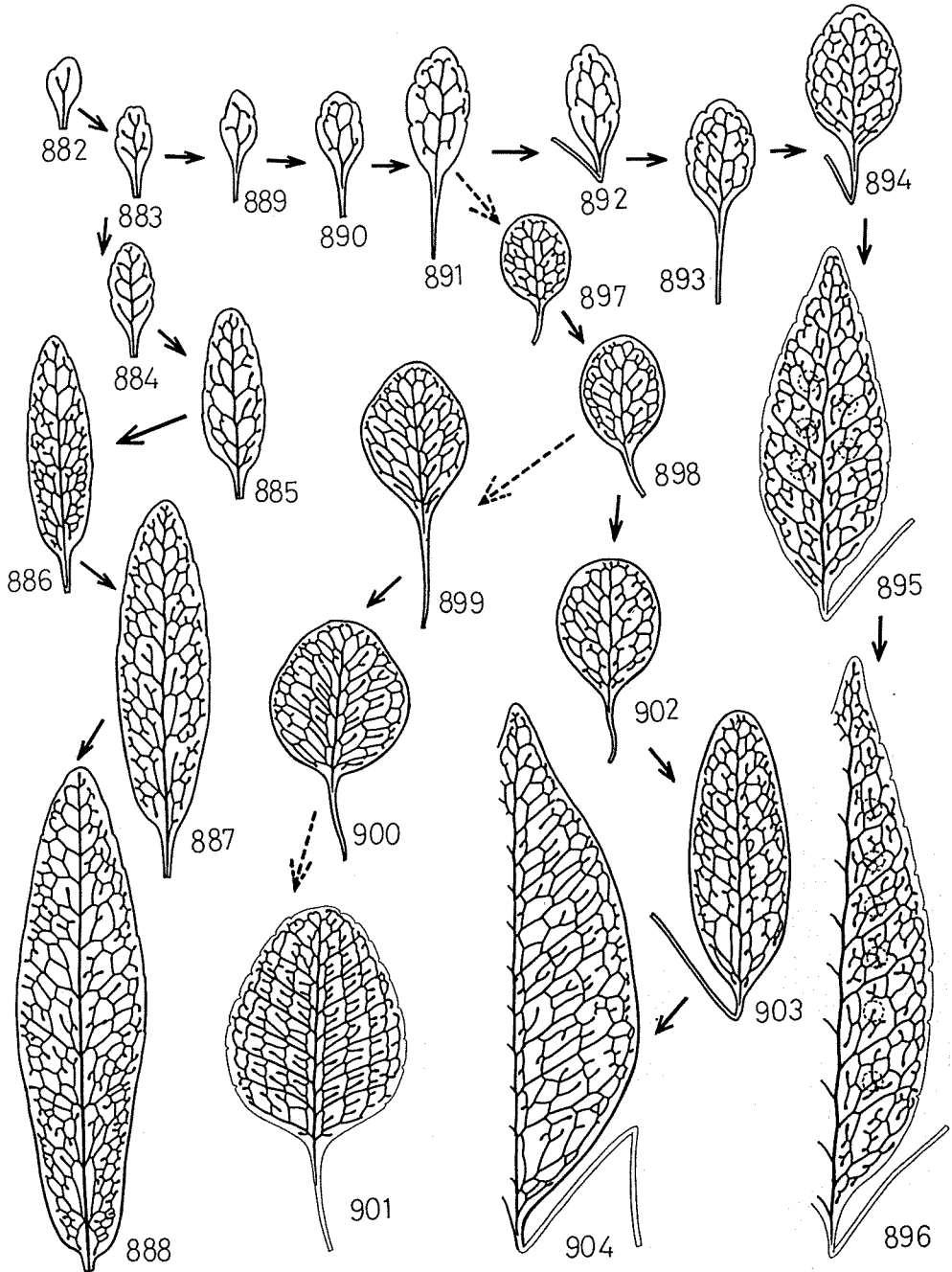
Figs. 815-839. Venation of *Pleopeltis*, *Campyloneurum* and *Pyrrosia*. 815-822: *Pleopeltis percussa*. 815, 816, 823-830: *Campyloneurum angustifolium*. 815, 816, 831-836: *Pyrrosia linearifolia*. 815, 816, 831-835, 837-839: *Pyrrosia lingua*.



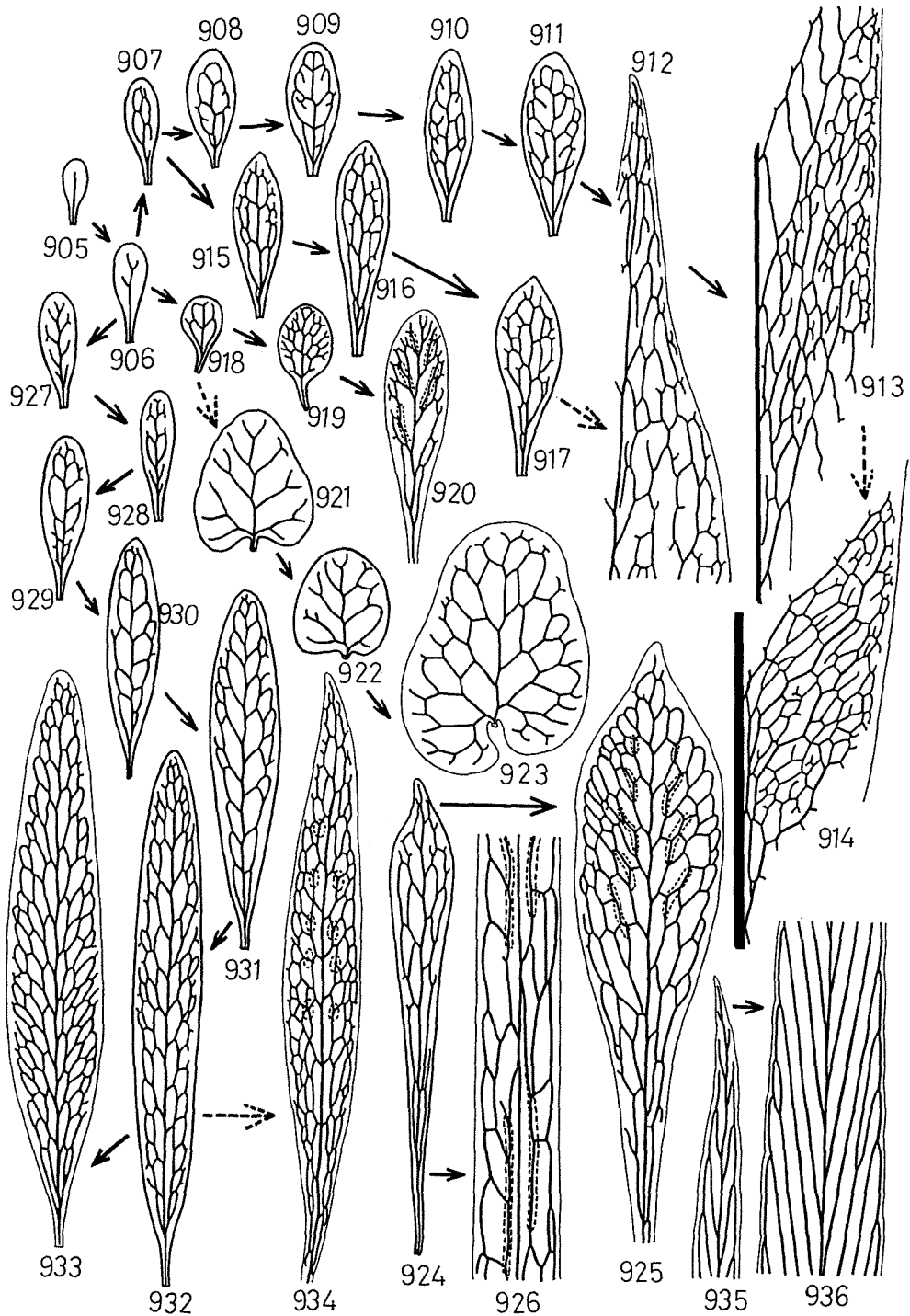
Figs. 840-860. Venation of *Microsorium* (including *Phymatodes*), *Lepisorus* and *Lemmaphyllum*. 840-848: *Microsorium punctatum*. 840, 841, 846-849: *M. (Phymatodes) vieillardii*. 840, 841, 846, 850: *M. (Ph.) soclopendria*. 840, 841-846, 851-852: *Lepisorus thunbergianus*. 840, 841, 853-860: *Lemmaphyllum microphyllum*.



Figs. 861-881. Venation of Drynarioid ferns. 861-870: *Drynariopsis heraclea* and most species of *Aglaomorpha*, *Drynaria* and *Pseudodrynaria*. 861-864, 871-874: *Drynaria rigidula*. 861, 862, 875-881: *Photinopteris acuminata*.



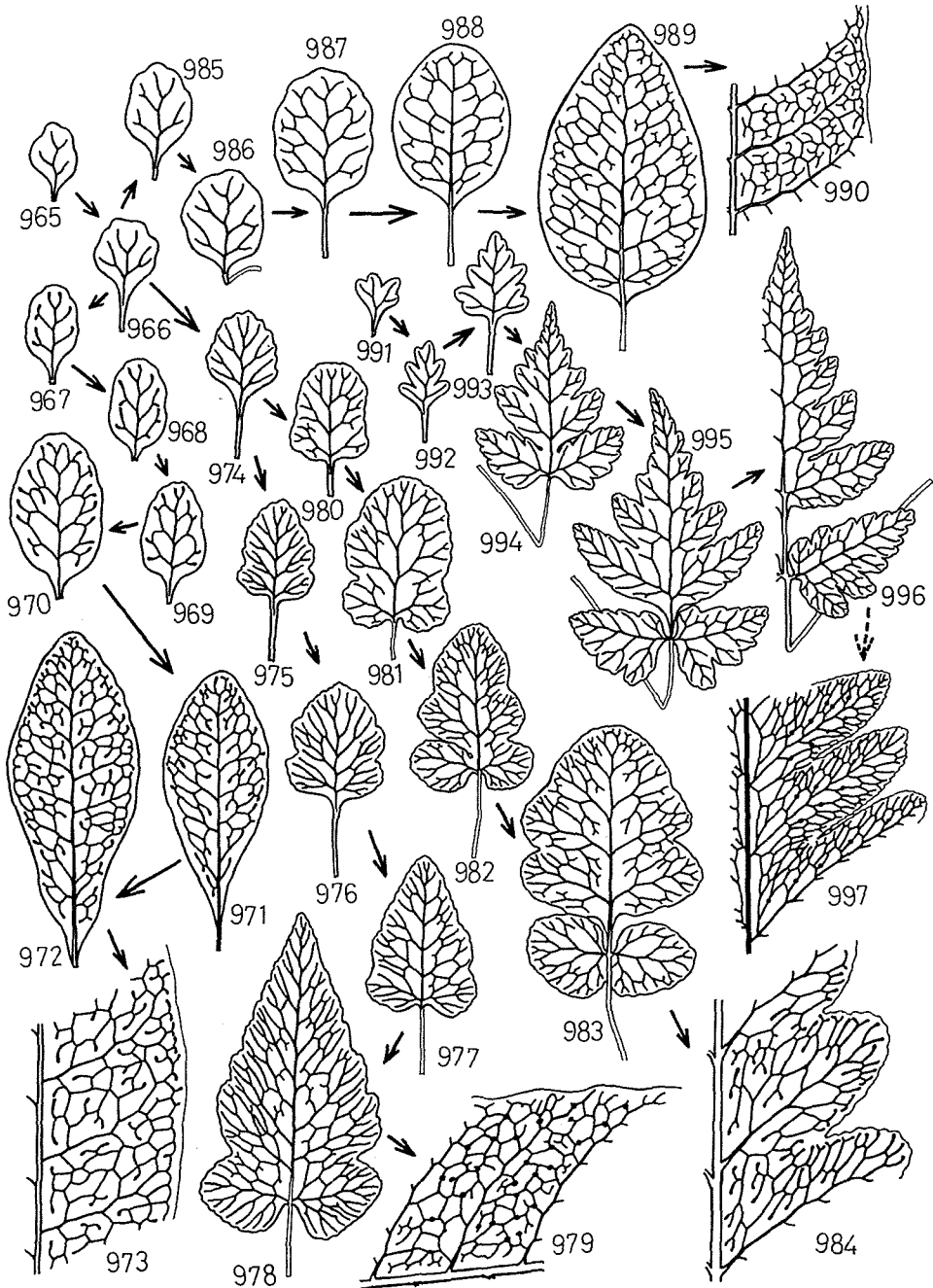
Figs. 882-904. Venation of Drynarioid and Crypsinoid ferns. 882-888: *Aglaomorpha meyeniana*. 882, 883, 889-896: *Crypsinus hastatus*. 882, 883, 889-891(-)897-898(-)899(-)901: *Pycnoloma metacoelum* and *P. murudense*. 882, 883, 889-891(-)897, 898, 902-904: *Selligaea heterocarpa*.



Figs. 905–936. Venation of *Loxogramme*, *Dictymia*, *Anarthropteris* and *Vittaria* (Vittariaceae). 905–914: *Loxogramme salicifolia* (913) and *L. nidiformis* (914). 905–907, 915–917: *L. duclouxii*. 905, 906, 918–920: *L. lankokiensis*. 905, 906, 918(–)921–923: *L. conferta*. (910), 924–925: *L. grammitoides*. (910), 924, 926: *L. subselliguea*. 905, 906, 927–933: *Dictymia mckeei*. 932, 934: *Anarthropteris lanceolata*. 935–936: *Vittaria amboinensis*.



Figs. 937-964. Venation of Dryopteridaceae subfam. Tectarioideae, well dissected species. 937-943: *Lastreopsis* sp. 944-950: *Ctenitis subglandulosa*. 944-946, 951-953: *Plecnemia irregularis*. 954-958: *Ctenitis eatonii*. 959-964: *Tectaria pseudo-sinuata*.



Figs. 965-997. Venation of Dryopteridaceae subfam. Tectarioideae, less dissected species. 965-973: *Tectaria decurrens*. 965, 966, 974-979: *Tectaria simonsii*. 965, 966, 974, 980-984: *Quercifilix zeilanica*. 965, 966, 985-990: *Hemigramma decurrens*. 991-996(-)997: *Tectaria gemmifera* (996) and *T. tenerifrons* (997).

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