

# MORPHOLOGY OF THE FERTILE LEAVES OF THE LOMARIOPSIDACEAE, WITH SPECIAL REFERENCE TO THE VENATION

By B. K. NAYAR

*Pteridology Laboratory, National Botanic Gardens, Lucknow, India*

(Received 1 October 1965)

## SUMMARY

Fertile pinnae of thirty-one species of the eight genera of Lomariopsidaceae studied have the lamina variously reduced, in some cases to narrow wings on either side of the midrib. The lamina is either broad, thin, and with the venation conspicuous on the surface, or narrow, fleshy, and with hidden venation. The mesophyll is undifferentiated and consists of thin-walled parenchyma which possesses collapsible walls in some species. Intercellular air spaces are inconspicuous in most species. The epidermal cells are usually thin-walled, chlorophyllous and dorsiventrally flattened. The midrib has two or three vascular strands which unite into one in the anterior half of the lamina. Distinct sclerenchyma tissue is absent: a few layers of thick-walled hypodermal cells occur in the midrib region in some.

Venation of the fertile pinna is almost similar to that of the sterile pinnae in *Bolbitis* and *Lomagramma* (both reticulate), and in *Egenolfia*, *Elaphoglossum* and *Thysanosoria* (all free-veined). The fertile pinnae of *Arthrobotrya*, *Lomariopsis* and *Teratophyllum* usually possess a reticulate venation, though the sterile pinnae are free-veined. A set of special veins supplying the sporangia is found in addition to the 'normal' venation in many species except *Elaphoglossum* and *Thysanosoria*. The special venation is variously developed in the different species of each genus; it consists of a set of veins close to the lower epidermis of the lamina and connected to the 'normal' veins at intervals: in some cases the special veins form extensive reticulations independent of the 'normal' venation. The two sets of veins are at different planes, one above the other. The special venation is not connected directly to the midrib and often has a longitudinal vein running parallel to the midrib on either side.

In all genera, except *Thysanosoria* which has discrete sori restricted to the vein tips, sporangia are acrostichoid in distribution. They are of the common leptosporangiate type. The sporangial stalk is slender and long in all, except *Lomagramma* and *Lomariopsis* in which it is short and stout. The stalk is three cells thick, the third row developed secondarily as a protrusion of the basal wall cell of the capsule in continuation of the stomium. Distinct paraphyses are absent, except in *Arthrobotrya*, *Lomagramma* and *Teratophyllum*.

The spores are bilateral, monolet and ranging in size from  $22 \times 33 \mu$  (*Bolbitis* spp., *Elaphoglossum* spp.) to  $90 \times 125 \mu$  (*Lomariopsis intermedia*). The exine is smooth except in *Lomagramma*, *Thysanosoria* (both granulose) and *Lomariopsis* spp. (spinulose). *Lomagramma* and *Thysanosoria* are perine-less; all others are perinate, with the perine bearing characteristic reticulate ornamentation in all except *Bolbitis* and *Elaphoglossum*.

## INTRODUCTION

The Lomariopsidaceae comprises eight genera of tropical ferns: *Arthrobotrya* (three species), *Bolbitis* (eighty-six species), *Egenolfia* (eleven species), *Elaphoglossum* (over 200 species), *Lomagramma* (fifteen species), *Lomariopsis* (forty species), *Teratophyllum* (eight species) and *Thysanosoria* (one species). The two large genera, *Bolbitis* and *Elaphoglossum*, are distributed in the tropics around the world; the next large genus, *Lomariopsis*, is also

comparatively widespread, occurring in East Asia, Africa and America. The others have limited geographical ranges restricted to East Asia, while the monotypic *Thysanosoria* is endemic to New Guinea. Apart from *Elaphoglossum*, which is mainly epiphytic, the family consists of terrestrial ferns usually inhabiting moist rocky forest beds, generally near streams, etc., in dense tropical forests.

The rhizome is epigeal, creeping and dorsiventral. Most genera are large scandent ferns with the rhizome climbing high over supports and bearing rather loosely placed leaves on the dorsal surface (away from the substratum). *Egenolfia*, *Elaphoglossum* and most species of *Bolbitis* are comparatively small plants with the rhizome short and bearing crowded leaves; some species of *Bolbitis*, like *B. heteroclita* and *B. subsimplex*, are high-climbing plants with elongated rhizomes and loosely placed leaves. The vascular cylinder of the rhizome is dictyostelic with the ventral half intact and gutter-shaped and the dorsal half dissected into a loose reticulum by closely placed large leaf gaps; roots are generally restricted to the ventral half. In some species of *Elaphoglossum* (Bell, 1950, 1951*b*) the ventral intact portion is inconspicuous and the vascular cylinder is nearly radiosymmetric and dictyostelic.

Leaves are arranged in three or more rows on the dorsal surface of the rhizome, except in *Teratophyllum* and many species of *Bolbitis*, *Egenolfia* and *Elaphoglossum* where they are in two rows. In *Bolbitis*, the climbing species and some of the large non-climbing ones (like *B. costata*) possess more than two rows of leaves on the adult rhizome; the comparatively large species of *Egenolfia*, like *E. bipinnatifida* and *E. vivipara*, possess three rows of leaves but most species possess only two rows. A vegetative bud and a root trace are found associated with the leaf base, the vascular connection to them originating from the abaxial end of the leaf gap, along with the leaf trace bundles (Bell, 1951*a*; Nayar and Kaur, 1964*a, b*, 1965*a, b*). Vascular connection to each leaf consists of many slender bundles forming a loose, gutter-shaped reticulum. The leaf lamina is pinnate, except in some species of *Lomagramma* and *Arthrobotrya* which are bipinnate, and *Elaphoglossum* with simple leaves. The juvenile leaves (bathyphylls) are different from the adult leaves (acrophylls) and are often bipinnate with small ultimate pinnules (*Bolbitis*, *Egenolfia*, *Teratophyllum*); such distinct juvenile leaves are absent in *Elaphoglossum* (Stokey and Atkinson, 1957) and *Lomariopsis* (Holtum, 1954). The lateral pinnae of the acrophylls are articulate to the rachis, except in *Bolbitis*, *Egenolfia* and *Elaphoglossum*. Venation is simple and free in all, except *Bolbitis* and *Lomagramma* which possess a reticulate venation; in the former there is a progressive simplification of the venation in the different species, the larger (and often climbing) species having a comparatively more complicated venation (Nayar and Kaur, 1964*a*).

Fertile leaves are produced seasonally and the fertile lamina is variously reduced in the different genera and species. In many species of *Elaphoglossum* it is scarcely smaller than the sterile lamina; in *Bolbitis*, some species (particularly the large climbing ones) possess broad fertile pinnae which are only slightly smaller than the sterile ones, whereas in the others the fertile lamina is highly reduced, the pinnae being narrowly linear (Copeland, 1928). Sporangia are borne all over the under surface of the fertile lamina in all, except *Thysanosoria* which has discrete sori. A special venation to supply the sporangia is reported in *Teratophyllum* (Holtum, 1937, 1938, 1954), but little is known regarding the fertile organs of the family. The present study is an attempt to fill this gap. A detailed account of the spore morphology of these ferns is being published elsewhere (Nayar and Kaur, 1965*c*).

## MATERIALS AND METHODS

The major difficulty in this kind of study is the non-availability of material, since the fertile leaves of many of these ferns are very rare and hard to obtain. I am therefore extremely grateful to Professor R. E. Holttum who personally obtained for me the fertile pinnae of most of these rare ferns from various herbaria of the world and thus made this study possible.

The study is based mostly on material obtained from herbarium specimens, except for the different species of *Bolbitis*, *Elaphoglossum* and *Egenolfia* which were collected fresh from the field. The thirty-one species (*Arthrobotrya*, one species; *Bolbitis*, ten species; *Egenolfia*, six species; *Elaphoglossum*, one species; *Lomagamma*, five species; *Lomariopsis*, four species; *Teratophyllum*, three species; and *Thysanosoria*, one species) used in this study are listed in the Appendix. As the identification of the bits of fertile material obtained from various herbaria could not possibly be verified by the author, details regarding all the materials used in this study are given in the Appendix to facilitate cross-checking if necessary.

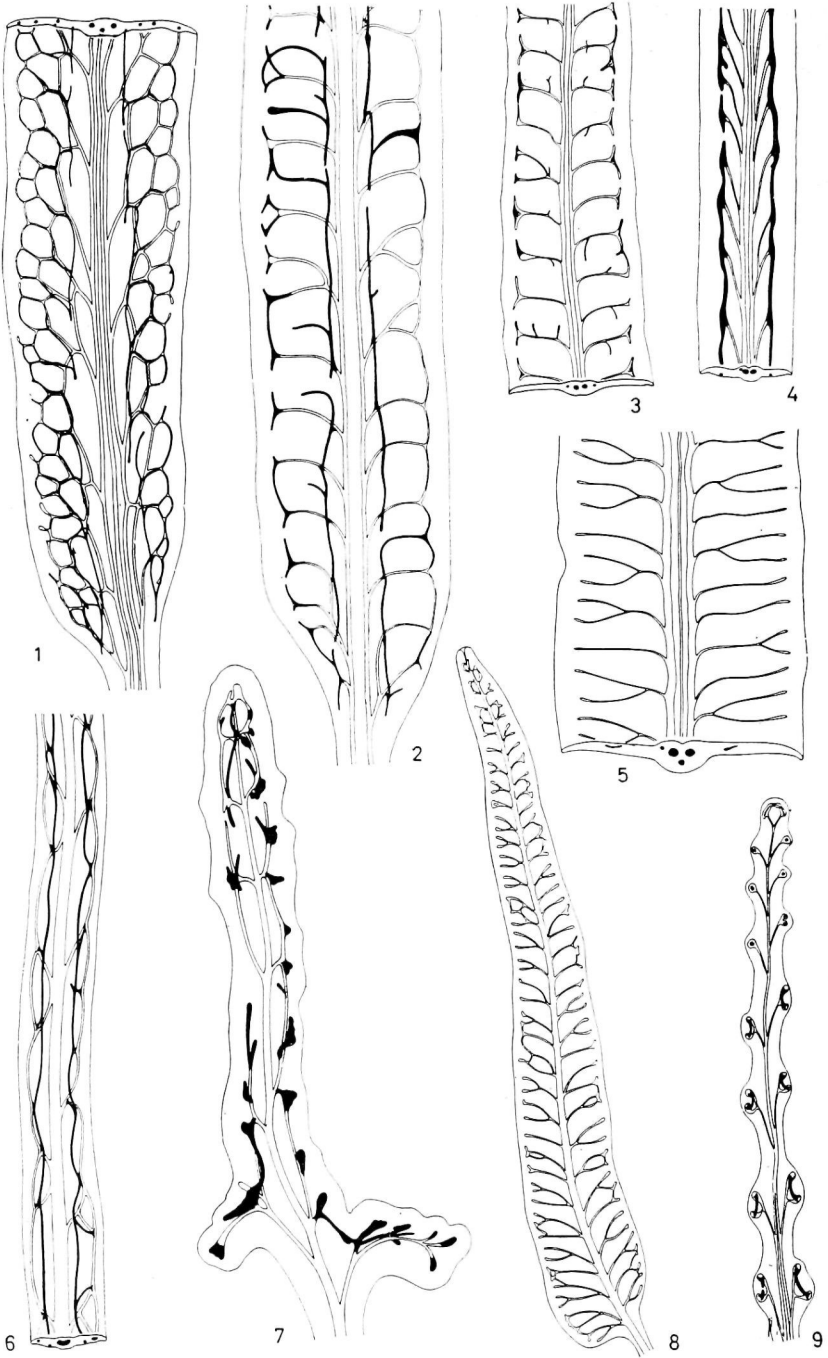
The fertile leaves were soaked in a 1% solution of basic fuchsin in 3% aqueous KOH, maintained at 60° C, with frequent changes of solution until the material is transparent. The cleared leaves were then washed in running water, and either studied directly or stored in 70% alcohol. Observations on anatomy are based either on fresh leaves, or on dried leaves soaked in 2% KOH at 60° C for 12–24 hours. Sections were cut at 10  $\mu$  thickness, using the common paraffin impregnation method; the sections were stained by safranin-fast green combination and mounted in Canada balsam. Observations on sporangia and paraphyses are based on either alcohol-preserved material or soaked ones mounted directly in glycerine. Morphological observations of spores are based on acetolysed preparations (method after Erdtman, 1952); methods of description and terminology used are the same as reported earlier (Nayar, 1964).

## OBSERVATIONS

*Fertile pinnae*

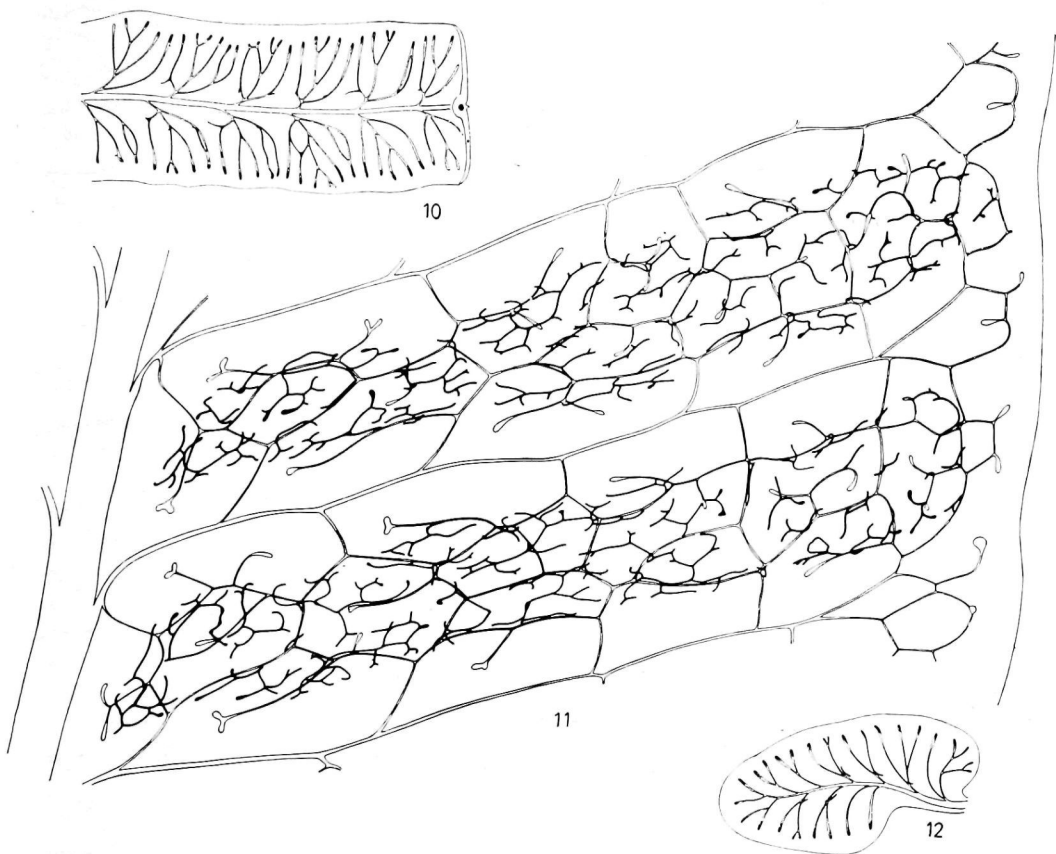
The fertile pinnae in all the genera of the family have the lamina variously reduced, sometimes into very narrow wings on either side of the midrib. In *Elaphoglossum*, some species of *Bolbitis* (*B. heteroclita*, *B. subsimplex*) and *Thysanosoria*, the fertile lamina is broad and little different in shape from the sterile ones, though slightly smaller in size. Sporangia are distributed all over the lower surface of the lamina except in *Thysanosoria* which has discrete, exindusiate sori restricted to the tips of the lateral veinlets. In the broad-leaved species of *Bolbitis*, like *B. heteroclita* and *B. subsimplex*, the sporangia are aggregated in broad bands between the main lateral veins. In some abnormal semi-fertile leaves of *B. subcrenata*, the sporangia may be grouped in nearly circular or variously elongated sori restricted to the points of fusion of the secondary veinlets of the lamina.

The fertile lamina is thin (100–150  $\mu$ ), resembling the sterile lamina in this respect in most species of *Bolbitis* and *Thysanosoria*; in the others it is thick and fleshy (usually 300–500  $\mu$ ), while some, like *Egenolfia sinensis*, *Lomagamma lomarioides*, *L. sinuata* forma *papuana*, *Lomariopsis kingii*, *L. intermedia* and *Teratophyllum ludens* have the lamina 600–800  $\mu$  thick. The marginal region of the lamina is usually devoid of any sporangia and is comparatively thin, forming narrow flanges often made up of the upper and lower



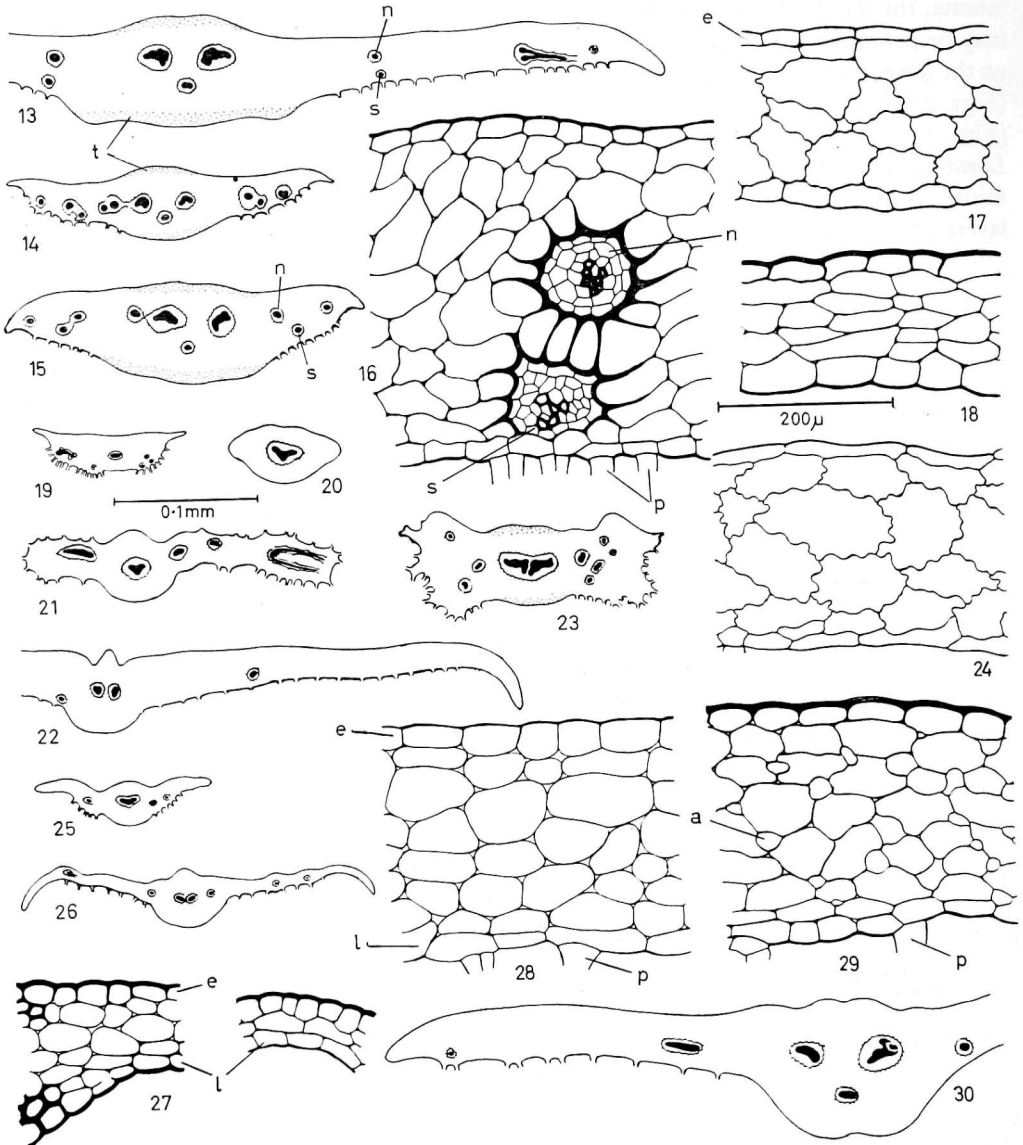
Figs. 1-9. Portions of the fertile lamina of the Lomariopsidaceae, showing venation pattern (the special veins spreading below the 'normal' veins are shown in black): 1. *Lomagramma sinuata*. 2. *Lomariopsis spectabilis*. 3. *L. cochinchinensis*. 4. *L. kingii*. 5. *L. intermedia*. 6. *Teratophyllum gracile*. 7. *Arthrobotrya articulata*. 8. *Teratophyllum arthropteroides*. 9. *Egenolfia vivipara*.

epidermis juxtaposed with no mesophyll tissue in between. In species with a thick fleshy lamina, the flange-like margin is clearly delimited (Figs. 14, 15, 19 and 23). The midrib may be prominent and protrude conspicuously on both the surfaces (more prominently on the lower), forming blunt ridges in species with comparatively thin broad fertile pinnae (Figs. 22, 25 and 26), or may be completely hidden as in those with fleshy narrow pinnae (Figs. 15, 19 and 23). In *Lomariopsis* the midrib is grooved on the upper surface. In *Lomagamma* the protruded midrib has a flat outer surface on both sides (so that the midrib is nearly tetragonal). When the midrib is prominent and protruded, two to four layers of hypodermal cells on either surface possess slightly thickened walls and are



Figs. 10–12. Portions of the fertile lamina of *Bolbitis* and *Egenolfia* showing venation pattern (the special veins are shown in black): 10. *E. sinensis*. 11. *B. subsimplex*. 12. *E. asplenifolia*.

rather elongated and narrow. The midrib usually has three vascular bundles, two large adaxial and one small abaxial, all of which merge into a single bundle in the anterior half of the pinna. In species possessing small pinnae the abaxial vascular strand is absent and the two adaxial ones may merge together near the base of the pinna as in *Arthrobotrya*. The endodermis of the vascular bundles is composed of large prominent cells with highly thickened radial and inner walls in species with narrow fleshy pinnae; in *Lomagamma sinuata* forma *papuan*a (Fig. 16) the thickening is very conspicuous and very deep brown



Figs. 13-30. Transverse sections of the fertile pinnae of the Lomariopsidaceae (a, intercellular air-space; e, upper epidermis; l, lower epidermis; n, vein of the 'normal' venation; p, sporangial stalk; s, special vein; t, thick walled cells). 13. *Lomagamma sinuata*, a portion of the pinna, showing midrib and lamina on one side. 14. *L. lomarioides*. 15. *L. sinuata* forma *papuana*. 16. Same, a portion showing cellular organization. 17. *L. sumatrana*, a portion showing cellular organization. 18. *Thysanosoria pteridiformis*, a portion showing cellular organization. 19. *Arthrobotrya articulata*. 20 and 21. *Egenolfia vivipara* (20, lamina-less region). 22. *E. sinensis*, a portion showing midrib and lamina on one side. 23. *Teratophyllum ludens*. 24. *T. arthropteroides*, a portion showing cellular organization. 25. *Bolbitis semicordata*. 26. *B. crispatula*. 27. Same, portions showing cellular organization. 28. *B. subsimplex*, a portion showing cellular organization. 29. *B. costata*, a portion showing cellular organization. 30. *Lomariopsis cochinchinensis*, a portion showing midrib and lamina on one side.

to blackish so that the vascular strands are visible even in untreated leaf material. The endodermal cells are small, irregular and thin-walled (except for faint thickenings like casparian bands on the lateral walls) in species possessing a thin lamina. The epidermis of the fertile pinnae, particularly the lower epidermis, consists of thin-walled cells with a sinuous contour, except the cells over the midrib and the main veins which are slightly thick-walled, narrow, and elongated parallel to the veins. In all the species studied, the epidermal cells are chlorophyllous. The cells are conspicuously flattened dorsiventrally where the pinna is fleshy and thick. In species possessing a thin fertile lamina the outer wall of the cells of the upper epidermis is faintly thickened (Figs. 18 and 27). The mesophyll is undifferentiated in all the species studied and is composed of thin-walled chlorophyllous parenchyma cells. In *Thysanosoria* (Fig. 18) and some of the thin-leaved species of *Bolbitis*, like *B. crispatula* (Fig. 27), the mesophyll consists of three to five layers of small, somewhat dorsiventrally flattened, densely chlorophyllous parenchyma cells with rounded corners and nearly straight sides. In most others the mesophyll is five to seven layered and the cells are large with small intercellular spaces. Large intercellular spaces and short-armed mesophyll parenchyma are found in some species of *Bolbitis*, like *B. costata* (Fig. 29). In species with a thick fleshy lamina there are often eight to twelve rows of rather sparsely chlorophyllous cells possessing thin sinuous walls (Fig. 17). In *Arthrobotrya*, *Lomagamma* (Fig. 17) and *Teratophyllum* (Fig. 24) the mesophyll consists of three to ten rows of conspicuously large, sparsely chlorophyllous cells with thin collapsible walls and nearly devoid of intercellular spaces. These cells are apparently water storing and collapse on wilting.

Hydathodes are present on the leaf lamina in some species. They are found regularly at or near the vein tips in *Thysanosoria* and may either be marginal or intramarginal on the upper surface. Hydathodes at the apices of veinlets are found in *Egenolfia vivipara* also. In *Bolbitis subsimplex* hydathodes are profuse and are located on the upper surface of the lamina where the free veins of the 'normal' venation terminate. In *Teratophyllum arthropteroides* there is an apical large hydathode in which the midrib terminates. The narrow fertile lamina of *Lomagamma sinuata* forma *papuana* bears a few protruded marginal hydathodes: there is often no direct vascular connection to these, but the mesophyll cells between the hydathode and the nearby vein are elongated, narrow and radially arranged.

The venation of the fertile pinna is largely similar to that of the sterile pinnae of the same species in the genera possessing a reticulate venation (*Bolbitis* and *Lomagamma*). In *Arthrobotrya*, *Lomariopsis* and *Teratophyllum*, though the sterile pinnae possess free veins, the venation is often reticulate in the fertile pinnae. *Egenolfia*, *Elaphoglossum* and *Thysanosoria* have free veins both in the fertile as well as in the sterile pinnae. A set of special veins supplying the sporangia is found in addition to the 'normal' veins of the fertile lamina in many of the species studied, except those of *Elaphoglossum* and *Thysanosoria*. This special venation is variously developed in the different species of each genus, and consists of a set of veins spreading close to the lower epidermis of the leaf and connected to the 'normal' veins at intervals; in some cases the special veins form extensive reticulations independent of the 'normal' venation. The two sets of veins are at different planes, one above the other, in the leaf lamina (Figs. 13, 16, 19 and 23), and are often separated from each other by ordinary leaf tissue. The special venation is not connected directly to the midrib and often has a pair of longitudinal veins running parallel to the midrib on either side. The morphology of the fertile pinnae, including the venation pattern in the different genera, is described below.

*Arthrobotrya*

The fertile leaves are bipinnate, with very small pinnules ( $4-7 \times 1$  mm, as against the sterile  $18 \times 7$  mm) having a blunt apex, irregular toothed margin and a large basal auricle on one side. The lamina is about  $300 \mu$  thick, except at the margins where it is suddenly narrowed into a thin narrow flange on either side. The midrib and the veins are completely hidden. A single, slender, rather dorsiventrally flattened vascular strand constitutes the midrib. The mesophyll is composed of large, nearly isodiametric, thin-walled cells and appears to be water storing. The endodermis of the midrib and the veins is ill-differentiated, but the cells possess band-like thickenings on the radial walls. There is no sclerenchyma tissue in the leaf, though two or three layers of hypodermal cells in the midrib region are smaller in size and regularly arranged. When the sporangia mature, the leaf lamina folds upward, the margins curling up. The venation (Figs. 7 and 47) is rather irregular, with the midrib bearing obliquely placed lateral veins on either side. The lateral veins are forked and the acroscopic and basiscopic branches of successive veins are fused to form a row of large areoles on either side of the midrib. The basal lateral vein supplying the auricle is pinnate and its branches may form reticulations. There is often no elaborate special venation to supply the sporangia, but short rather diffuse branches originating superficially from the lateral veins extend towards the lower epidermis and spread below it to supply the sporangia. In some cases, some of these branches from nearby veins coalesce to form vascular commissures adjacent to the lower epidermis; rarely, an interrupted special vein may be formed by the development of regular commissures between sets of nearby branches.

*Bolbitis*

The fertile leaves are pinnate, with the lamina exhibiting different degrees of reduction depending on the species. The lamina is thin (usually  $200-300 \mu$ , but as thin as  $70-100 \mu$  in some such as *B. crispatula*), with the midrib and main veins protruded on the lower surface. The epidermal cells over the midrib and the veins are thick-walled and elongated. Both the epidermises are chlorophyllous, and the outer wall of the upper epidermis is thickened in most species. The mesophyll tissue consists usually of four to six rows of cells: the thickness of the lamina depends upon the size of the mesophyll cells rather than on the number of rows of cells constituting the mesophyll. In the thin-leaved *B. crispatula* (Fig. 27) and *B. semicordata*, the mesophyll cells are comparatively small and rather flattened dorsiventrally. The mesophyll cells are large, nearly isodiametric, with straight walls and small intercellular spaces in *B. heteroclita* and *B. subsimplex* (Fig. 28), both of which possess a broad, comparatively thick fertile lamina. In *B. costata* the mesophyll cells are 'armed', having large intercellular spaces (Fig. 29). The endodermis of the vascular bundles in most species is composed of large cells with conspicuously thickened inner and radial walls; in some species, such as *B. costata*, the endodermis is not well differentiated and is composed of small thin-walled cells.

The venation of the fertile pinnae is almost similar to that of the sterile ones of the same species (often having several rows of characteristic areoles on either side of the midrib). In *B. subsimplex* in which the fertile pinnae are broad, lanceolate and little different from the sterile ones, the midrib bears prominent, obliquely placed, alternating main lateral veins on either side, extending almost to the margin and the successive ones connected together at regular intervals by zigzag secondary veins to form a series of large primary areoles (Figs. 11 and 50). Tertiary veins parallel to the main lateral veins divide each primary areole into three secondary areoles of which the middle one is broader and



sometimes further divided transversely as in the sterile leaves; the costal primary areoles are undivided. Each ultimate areole (including the costal ones) encloses a free veinlet which is sometimes forked, with the branchlets spreading in different directions. The vascular tissue towards the tips of these branchlets is rather diffuse, and enters hydathodes on the upper surface of the lamina. A set of special veins below the 'normal' venation supply the sporangia. These are restricted to the broad fertile areas of the leaf, between successive main lateral veins (not extending either to the midrib or to the main lateral veins). The special venation consists of slender veinlets originating as superficial branches from the veins of the second, third or fourth order of the 'normal' venation and extending to the lower epidermis of the lamina where they spread irregularly and branch profusely forming clusters of shaggy slender veinlets. Irregular areoles are also sometimes formed by these veinlets. Vertical vascular commissures connect the two sets of veins here and there. Contrary to the special veins found in other *Lomariopsidaceae*, which run mostly parallel to the 'normal' veins above (appearing like a mirror image of the latter), those of *B. subsimplex* spread irregularly as in *Christiopteris tricuspis* (Bower, 1928). Also, these special veinlets are more numerous than the 'normal' veins above, though more slender.

*Bolbitis heteroclita* and *B. costata* are similar to *B. subsimplex* in the form and size of their fertile pinnae, but an elaborate special venation as found in the latter is absent in them. The 'normal' venation is similar to that of the sterile pinnae, having three rows of irregular areoles between successive main lateral veins and with the ultimate areoles rarely having free included veinlets (Figs. 51 and 52). However, a short superficial branch may occasionally be borne on some of the tertiary veinlets, recalling the special venation of *B. subsimplex*. These branches are short, inconspicuous and infrequent so that they may be easily overlooked, but they do extend to the lower epidermis. Also, similar short superficial branches occur in the fertile leaves of *B. presliana*; as in *B. heteroclita*, the fertile lamina in this species is broad and scarcely different from the sterile one. The venation is similar to that of the sterile pinnae, often having two rows of goniopteroid areoles on either side of the midrib (each areole connecting the successive main lateral veins). The vascular tissue at the tips of the free veinlets is diffuse and slightly tilted towards the lower epidermis; hydathodes are absent. The special branches are borne on some of the secondary veins in the basal half of the lamina.

In the other species of *Bolbitis* studied, the lamina of the fertile pinnae is reduced to narrow wings on either side of the midrib. The venation is similar to that of the sterile pinnae of the respective species, though simpler. There is often one (or two) row of areoles on either side of the midrib (Fig. 53), and the areoles extend less than three-quarters of the way to the margin. There is no special venation to supply the sporangia.

### *Egenolfia*

The fertile pinnae of *Egenolfia* possess a reduced lamina which may either be broad, as in *E. appendiculata*, *E. asplenifolia*, *E. keralensis*, *E. bipinnatifida* and *E. sinensis*, or reduced to inconspicuous lobes (at the regions of the lateral veins) on either side as in *E. vivipara*. It is rather thick and fleshy in all species, with the venation nearly hidden, except for the midrib which is protruding on the lower surface. Two or three vascular strands (which merge into one in the anterior half of the pinna) constitute the midrib. The endodermis of the vascular strands may be ill-differentiated, composed of small thin-walled cells as in those possessing broad pinnae, or may be well-differentiated and composed of large cells with prominently thickened inner and radial walls as in those with highly reduced fertile lamina (*E. vivipara*). The margins of the fertile lamina are gradually

thinner in the broad-leaved forms; the margin is broad and thick in the others, and bears hydathodes on the upper surface at the regions of the vein endings. On the highly reduced fertile lamina of *E. vivipara*, sporangia occur all over the lower and upper surfaces of the lobes as well as on the margins. The mesophyll consists of large isodiametric cells with sinuous outline and large intercellular spaces in species possessing a broad lamina; the epidermal cells are smaller in size compared to the mesophyll cells, and are thin-walled and chlorophyllous. In the fertile lobes of *E. vivipara*, the mesophyll cells are rather elongated parallel to the veins and possess inconspicuous air spaces.

The venation of the fertile pinnae of *Egenolfia* is free as in the sterile pinnae, with the midrib bearing alternate lateral veins on either side, extending nearly to the margins. In *E. appendiculata* and *E. asplenifolia* (Fig. 12) the lateral veins are forked once, with the branchlets possessing dilated apices which are tilted slightly towards the lower surface (but often not extending to the lower epidermis); in *E. bipinnatifida*, *E. keralensis* and *E. sinensis* the lateral veins are pinnately branched and irregular reticulations are rarely formed towards the base of the pinnae (Figs. 10 and 54). There is no trace of any special veins in *E. keralensis* but occasional, short, faint, superficial branchlets extending to the lower epidermis are borne by some of the main lateral veins in the others. These veinlets are very feeble and, in *E. asplenifolia*, are sometimes forked towards the tips (Fig. 12).

In *E. vivipara*, in which the fertile lamina is highly reduced, the midrib bears alternately placed oblique lateral veins which are forked towards the apex, with the branches diverging from each other. The vascular tissue at the tips of the branches is diffuse and spreading markedly. There is a prominent hydathode on the upper surface of the lamina at each vein-ending. A special vascular commissure running close to the lower epidermis (on a plane below the 'normal' veins) connects the tips of the veinlets (Figs. 9 and 48). This commissure is C-shaped, with the concavity facing away from the midrib. Towards the anterior end of the fertile pinna the lateral veins of the midrib are very short and not forked, but their tips are considerably dilated, with the vascular tissue extending to the lower epidermis.

### *Elaphoglossum*

Only one species, *E. conforme*, has been studied. The fertile lamina is broad and little different from the sterile in shape, size and venation. The midrib bears closely placed lateral veins perpendicular to it and forked once or twice, with the branches nearly parallel to each other and extending almost to the margin. The vascular elements at the tips of the veins are diffuse and spreading. All veins are free and there is no special venation or hydathodes.

### *Lomagrumma*

The lamina of the fertile pinnae is markedly reduced, being much narrower than that of the sterile pinnae. In some species like *L. sinuata* and *L. sumatrana* they are up to a centimetre broad (as against the sterile pinnae which are about 4 cm in *L. sinuata* and 2 cm in *L. sumatrana*) and lanceolate in shape, whereas in the others it is linear with the lamina 2-3 mm broad. The fertile lamina is 300-400  $\mu$  thick in all the species studied and rather fleshy. The margins may be thin (composed of contiguous epidermal cells only) as in *L. sumatrana* and *L. perakensis* or as thick as the other regions of the lamina and rounded. The midrib is prominent, forming broad blunt ridges on both the surfaces (about 1.5 mm broad and 1.0 mm thick). A ribbon-like band of rather thick-walled sclerenchymatous cells, three or four cells thick, occur hypodermally on either surface.

There are usually three vascular bundles in the midrib, the two near the upper surface being conspicuously larger than the one below. The endodermis of the vascular strands is thin-walled, except for the faint band-like thickenings found on the radial walls. Both the upper and lower epidermis consists of small cells flattened dorsiventrally. The mesophyll is undifferentiated and composed of large, thin-walled parenchymatous cells with collapsible walls and small intercellular air spaces. Generally the cells near the upper epidermis are slightly larger in size.

As in the sterile leaves, the venation is reticulate with a prominent midrib. The lamina on either side has an elaborate special venation to supply the sporangia. The special venation usually appears like a mirror image of the 'normal' venation above, and both the sets of veins merge into one at the region of the marginal areoles. Towards the midrib the special venation ends abruptly in a longitudinal vein running parallel to the midrib on either side. The 'normal' venation in the broad-leaved species (*L. sinuata*, *L. sumatrana*) consists of three rows of polygonal areoles on either side of the midrib (Figs. 1 and 44). The costal areolés are large, extending from one main lateral vein to the next; the second and third rows of areoles are progressively smaller, two or three of the marginal areoles corresponding with one areole of the middle row and two or three of the middle row corresponding with each of the costal row. Free included veinlets are absent. Some of the marginal areoles are incomplete, so that there is no regular intramarginal vein. The special veins are also reticulate like the 'normal' veins and are placed close to the lower epidermis of the lamina, each areole corresponding to an areole of the upper row. The costal set of areoles of the special venation is often irregular, the areoles being narrower and sometimes incomplete on the costal side. The two sets of areoles (those of the special venation and those of the 'normal' venation) are connected together regularly by vertical vascular commissures at the corners of the areoles. Rarely, some of the areoles of the special venation possess included free-ending veinlets. In *L. sinuata* (Fig. 1) the special venation usually consists of one irregular row of areoles matching with the second row of areoles on either side of the midrib of the 'normal' venation. Occasional branches from this towards the midrib may run for a short distance parallel to the midrib, but never forms a costal vein as in *L. sumatrana*.

In the other species of *Lomagrumma* investigated (*L. lomarioides*, *L. perakensis*, and *L. sinuata* forma *papuana*) the lamina of the fertile pinnae is reduced to narrow wings, usually only as broad as the midrib itself (Figs. 14 and 15). The venation is reticulate, as in the broad-leaved species, but the areoles are very narrow and elongated along the costa. Beyond the costal areoles, there is usually only one row of areoles in *L. perakense* and one or two rows in the others (Fig. 43). The special vein in *L. perakensis* rarely forms areoles, but is usually represented as an elongated irregular vein parallel to the midrib on either side and regularly connected to the outer row of areoles. In the others a row of areoles parallel to the second row of 'normal' areoles, and connected to the marginal areoles as in *L. sumatrana*, is found.

### *Lomariopsis*

Among the different species of *Lomariopsis* there is a progressive reduction in the breadth of the fertile lamina and in some, like *L. intermedia* and *L. cochinchinensis*, the lamina is 15–20 cm long and 2 cm broad (as against 20 × 5 cm for the sterile lamina). Though the sterile pinnae in all the species possess free veins, most species possess a reticulate venation in the fertile pinnae. A set of special veins is found in all the species studied, except for *L. intermedia* where the venation is free (Fig. 5). The midrib in this

species bears alternately placed main lateral veins perpendicular to it which are forked once, with the branches parallel and extending nearly to the margin (as in *Elaphoglossum*). In *L. cochinchinensis* (Fig. 3) the lateral veins are more prominent, with the vascular elements loosely placed and spreading at the tips of the veins. The tips of the veins are tilted towards the lower epidermis and the vascular elements spread perpendicular to the veins, close to the lower epidermis, extending parallel to the margins and sometimes forming intramarginal vascular commissures between successive veins. Some of the lateral veins bear towards their middle a superficial, short, feeble branch extending to the lower epidermis as in *Egenolfia* spp.; these branchlets are usually unbranched and run parallel to the midrib close to the lower epidermis. Rarely more than one such superficial branch may be found on a lateral vein, but many lateral veins are devoid of such branches.

In *Lomariopsis kingii*, in which the fertile lamina is very narrow, the lateral veins are forked as in *L. cochinchinensis* but are oblique to the midrib, and the vascular commissures form an intramarginal vein placed close to the lower epidermis (Fig. 4). *L. spectabilis* (fertile pinnae  $24 \times 0.4$  cm, sterile pinnae  $20-25 \times 1.5-2.0$  cm) has the fertile pinna with a similar vein arrangement as in *L. kingii*, but the lateral veins regularly bear superficial branches (Figs. 2 and 45). These branches are borne as in *L. cochinchinensis* but are more prominent, and those from successive lateral veins are fused together; there is thus a regular longitudinal special vein parallel to the midrib and conspicuously below the plane of the 'normal' veins. This special vein bears excurrent branches (often from the region equidistant from the main lateral veins on either side) pointing away from the midrib and parallel to the main lateral veins. Some of these branches extend and fuse with the intramarginal vein connecting the tips of the main lateral veins; in such cases these branches resemble the main lateral veins and are thus easily overlooked. Extra superficial branches are also borne on some of the main lateral veins, recalling the condition in *L. cochinchinensis* and *Egenolfia* spp.

### *Teratophyllum*

As in *Lomariopsis*, the lamina of the fertile pinnae exhibit different degrees of reduction in the different species. In *Teratophyllum arthropteroides* the fertile pinna is broad, nearly of the same size as the sterile ones ( $5-9 \times 1.5-2.0$  cm), with the lamina thin ( $200-250 \mu$ ) and with the midrib and the main lateral veins raised on the lower surface. The epidermis is thin-walled and composed of large dorsiventrally flattened, sparsely chlorophyllous cells. The mesophyll consists of three or four rows of large cells nearly devoid of intercellular spaces, sparsely chlorophyllous and possessing thin collapsible walls, and which are probably water storing. The endodermis of the veins consists of large cells with prominently thickened inner and radial walls. The venation (Figs. 8 and 46) is similar to that in the sterile leaf and there are no special veins to supply the sporangia. The midrib bears alternating lateral veins on either side which are slightly oblique and usually forked once. The vascular tissue at the tips of the veins spreads slightly or may sometimes be forked, with the branches of nearby veins often fused to form an intramarginal commissure as in *Lomariopsis cochinchinensis*. The midrib extends to the tip of the leaf where it ends in a funnel-shaped, large, terminal hydathode.

The fertile pinnae are very narrow, thick and fleshy in *Teratophyllum ludens* and *Teratophyllum gracile* (1-2 mm broad compared to 1.0-1.5 cm for the sterile pinna in *T. gracile* and 2-4 cm in *T. ludens*). Structurally they are similar to the fertile pinnae of those species of *Lomagramma* possessing a reduced fertile lamina (*L. sinuata* forma *papuan*). The venation is similar to that of the narrow-leaved species of *Lomariopsis*,

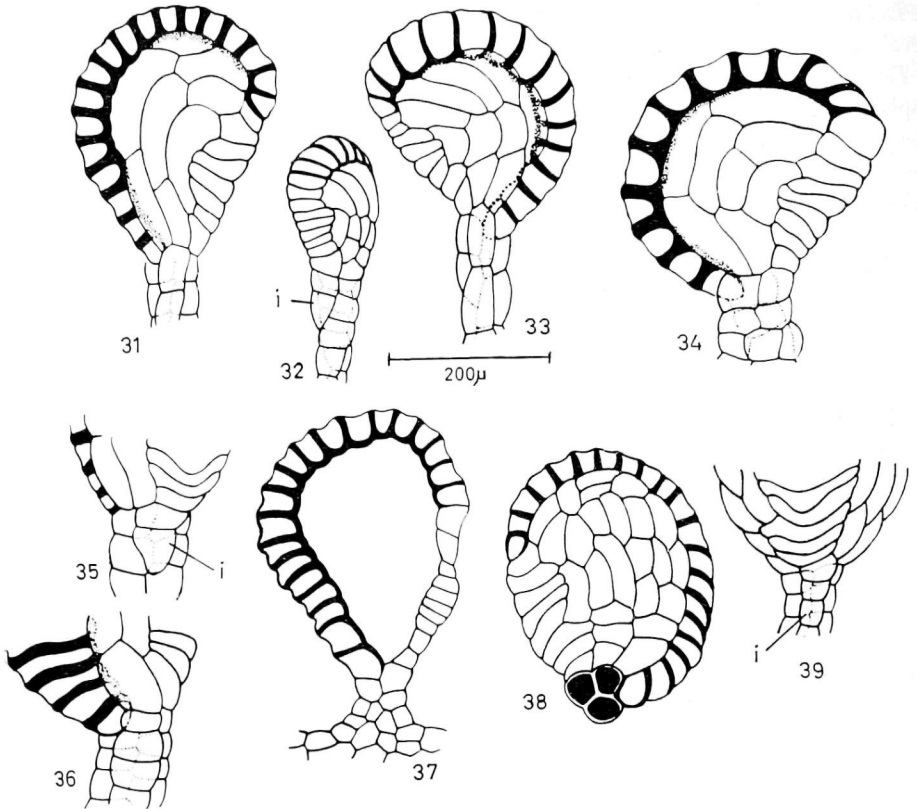
like *L. kingii*, with a regular intramarginal vein connecting the tips of the obliquely placed lateral veins (Fig. 4), so that there is a series of large areoles on either side of the midrib. In *Teratophyllum gracile* some of the lateral veins are forked. A set of special veins, supplying the sporangia and placed close to the lower epidermis is found in both *T. ludens* and *T. gracile* (Figs. 6 and 49). This consists of an elongated slender vein on either side of the midrib and connected to the 'normal' lateral veins by short vertical commissures at the points where the lateral veins unite with the intramarginal commissure. In addition, there is an excurrent branch of the special vein regularly between successive lateral veins of the 'normal' venation, connecting the special vein to the intramarginal vein as in *Lomariopsis cochinchinensis*, but more regular than in the latter. Like the special vein on either side of the midrib, these branches run close to the lower epidermis.

### *Thysanosoria*

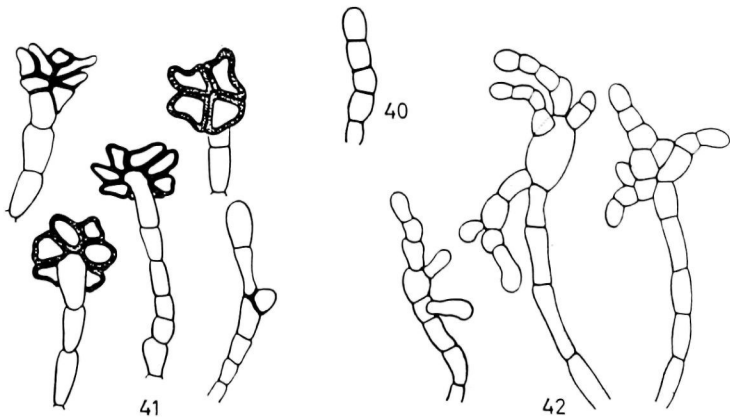
The monotypic genus *Thysanosoria* is the only member of the *Lomariopsidaceae* possessing discrete sori. The fertile lamina is broad (over 2 cm), and there is no special venation to supply the sorus. The lamina is thin, with the midrib protruded on either side. The mesophyll tissue consists of three or four rows of rather dorsiventrally flattened parenchyma cells with nearly straight sides and very inconspicuous intercellular spaces (Fig. 18). The outer wall of the upper epidermis is slightly thickened. The epidermal cells are larger in size compared to the mesophyll cells and all cells (including those of both the epidermises) are densely chlorophyllous. The midrib bears alternately placed lateral veins on either side as in the sterile pinnae and all veins extend close to the margin. The sorus is circular and seated over the tip of the vein on the lower surface. As in some species of *Egenolfia*, there is a prominent hydathode opposite the sorus on the upper surface, supplied by vascular tissue from the tips of the veins. In some cases the hydathode is marginal instead of superficial; the vascular tissue does not then extend up to the hydathode, and the parenchymatous tissue between the vein tip and the hydathode is composed of elongated, slender cells different from the other cells of the leaf.

### *Sporangia and Paraphyses*

In all the species studied, the sporangia (Figs. 31-39) are of the common leptosporangiate type. The sporangial stalk is short and stout in *Lomagrumma* and *Lomariopsis*; in *Teratophyllum*, *Arthrobotrya* and *Thysanosoria* the stalk is slightly longer and in *Bolbitis*, *Egenolfia* and *Elaphoglossum* the stalk is slender and as long or longer than the capsule. In most cases the base of the stalk is dilated towards the placentum, often appearing conical and sometimes four or five cells thick. The sporangial stalk is generally three cells thick, with two rows of cells continuous with the lateral faces of the capsule (with the end of the annulus wedged between the two rows on one side) and the third row continuous with the stomium. The stalk is often rather twisted in mature sporangia. In *Bolbitis*, *Egenolfia* and *Elaphoglossum* (in which the sporangial stalk is long) the third row of stalk cells (the row continuous with the stomium) is shorter than the other two and does not extend to the base. It is formed secondarily during sporangial development, as a downward protrusion of the basal wall cell of the capsule (Nayar and Kaur, 1965a). In some species the third row is represented by a single short cell, whereas in the others it is two or three cells long and extends half way or more to the base of the stalk. In *Thysanosoria* the third row may be either short and then composed of two cells which extend a little more than half way down the stalk, or may be extending to the base. The third row, as in *Bolbitis*, etc., is formed secondarily during sporangial development



Figs. 31–39. Sporangia of the Lomariopsidaceae (i, the secondarily developed third row of stalk cells). 31. *Lomagamma sinuata* forma *papuana*. 32 and 33. *Thysanosoria pteridiformis* (32, young sporangium). 34–36. *Lomariopsis spectabilis*. 37. L.s. of sporangium of *Teratophyllum ludens*. 38 and 39. *Arthrobotrya articulata*.



Figs. 40–42. Paraphyses. 40. *Arthrobotrya articulata*. 41. *Lomagamma lomarioides*. 42. *Teratophyllum gracile*.

(Fig. 32, i). In the other genera, the sporangial stalk is usually three cells thick throughout, the third row extending from the capsule base to the placentum, except occasionally in *Lomariopsis* where the third row may be short as in *Thysanosoria* (Fig. 35, i).

Distinct paraphyses are absent in *Bolbitis*, *Egenolfia*, *Elaphoglossum*, *Lomariopsis* and *Thysanosoria*; foliar hairs similar to those found on the sterile lamina are, however, found mixed with the sporangia. These hairs are uniseriate, multicellular and club-shaped. In *Arthrobotrya* the foliar hairs on the fertile lamina are larger than those on the sterile and are four to six cells long, composed of slender elongated cells and with the terminal cell slightly swollen (Fig. 40). Paraphyses are profuse in *Teratophyllum* and *Lomagamma*. In the former, the paraphysis (Fig. 42) consists of a long slender uniseriate stalk (composed of five to eight thin-walled cells) having a swollen, usually multicellular head bearing several shaggy branches which spread in an umbrella-like fashion. The branches are two to four cells long, rarely divided, and with the terminal cell having dense brown contents. Unbranched foliar hairs, similar to those found in *Arthrobotrya*, also occur mixed with the branched paraphyses. The paraphyses of *Lomagamma* (Fig. 41) are characteristic in possessing a multicellular, peltate, plate-like apex borne on a long, uniseriate, slender, thin-walled stalk, five to eight cells long. The terminal plate consists of three to eight flattened, wedge-shaped cells arranged in a radial manner. The stalk is thin-walled while the shield-like apex consists of thick-walled, dark brown to blackish cells. Rarely, some of the paraphyses lack a peltate apex and may terminate in a club-shaped cell, thus resembling the paraphysis of *Arthrobotrya*; sometimes some of these paraphyses are branched, bearing one or two branches, resembling some of the simpler paraphyses of *Teratophyllum*.

#### Spores

Spores of the Lomariopsidaceae are of the bilateral type with a monolete laesura which is usually tenuimarginate but in some species possesses faintly thickened inner margins. There is a wide range in size, the spores of some species of *Lomariopsis* being the largest so far known among the homosporous ferns (in *L. intermedia* they measure  $125\ \mu$  exclusive of the perine, and they are nearly  $200\ \mu$  across in the equatorial plane, including the perine). The smallest spores are found in some species of *Bolbitis* and *Elaphoglossum* (in *Bolbitis sculpturata* the mean dimensions are  $22 \times 32\ \mu$ , with a range  $18\text{--}26 \times 30\text{--}34\ \mu$ ; in *B. subsimplex*  $23 \times 34\ \mu$ , with a range  $20\text{--}24 \times 32\text{--}40\ \mu$ ; in *Elaphoglossum crinitum*  $22 \times 31\ \mu$ , with a range  $18\text{--}28 \times 28\text{--}35\ \mu$ ). In general the spores of *Bolbitis* are  $30 \times 42\ \mu$  in size, those with larger spores being *B. costata* ( $34 \times 45\ \mu$ ), *B. diversifolia* ( $36 \times 48\ \mu$ ), *B. heudeloti* ( $40 \times 55\ \mu$ ) and *B. crispatula* ( $32 \times 40\ \mu$ ). The spores of *Egenolfia* are about  $32 \times 43\ \mu$  in size, *E. appendiculata* and *E. asplenifolia* have larger spores. In *Arthrobotrya* the spores are much larger, being on an average  $50 \times 70\ \mu$ . In *Teratophyllum* they are  $40\text{--}58 \times 52\text{--}82\ \mu$  in size, those like *T. arthropteroides* having comparatively smaller spores ( $30 \times 52\ \mu$ ) and *T. gracile* having large spores ( $58 \times 82\ \mu$ ). The maximum range of size is in *Lomariopsis*, some like *L. guineensis* having spores averaging  $30 \times 43\ \mu$  as in *Egenolfia*, while others like *Lomariopsis intermedia* having spores  $90 \times 125\ \mu$ . Most other species, however, have spores  $45\text{--}51 \times 62\text{--}76\ \mu$  in size.

The exine is  $2\text{--}4\ \mu$  thick, and it is smooth except in *Lomagamma* and *Thysanosoria* in which it is variously granulose, and in some species of *Lomariopsis* (*L. decrescens*, *L. guineensis*) in which it is densely spinulose. There is a distinct perine in all except *Lomagamma* and *Thysanosoria*, both of which lack perine. The perine bears a characteristic, fine reticulate ornamentation (with the polygonal meshes  $2\text{--}3\ \mu$  across and the muri often

less than 1–2  $\mu$  broad and high) in *Arthrobotrya*, *Egenolfia*, *Lomariopsis* and *Teratophyllum*; in some species, like *T. ludens*, *Lomariopsis kingii* and *L. intermedia*, the muri of the reticula are interrupted, appearing like rugulae arranged regularly to present a reticulate pattern. The reticulations are very prominent, having broad (up to 6  $\mu$ ) muri bearing spinules (3–7  $\mu$  long) in *L. guineensis*; the lumina is then reduced to irregularly circular areas, 1.5–3  $\mu$  across. In *Egenolfia*, some species such as *E. appendiculata* and *E. asplenifolia* possess prominent reticulation whereas in others, such as *E. bipinnatifida* and *E. sinensis*, it is very faint. The perine is sometimes perforated, having small circular or ovate lacunae irregularly scattered and rather sparse. In *Bolbitis* and *Elaphoglossum* the perine is variously granulose; some species such as *Bolbitis heteroclita* and *B. subsimplex* have very faint granulae whereas others such as *B. acrostichoides* and *B. presliana* have prominent granulae often coalesced together to form rugulae and sometimes irregular reticulate patterns. The perine forms a loose cover (up to about 50  $\mu$  as in *Lomariopsis intermedia*) which is prominently wrinkled into elongated, sinuous folds, except in some species of *Bolbitis* and *Elaphoglossum*. In most species of *Egenolfia*, the folds are crowded and rather faint. In *Elaphoglossum*, the perine is rather adherent to the exine and wrinkled either into many crowded elongated folds possessing prominently undulated crests, or into short subconical folds; in some species it is very closely adherent and skin-like (Stokey and Atkinson, 1957). *Bolbitis* exhibits a good deal of variation among the different species in the nature of the perine. In many species, such as *B. subsimplex*, *B. heteroclita* and *B. diversifolia*, the perine is loose and wrinkled into lobate folds resembling the perine of *Lomariopsis* and *Teratophyllum*. In some others, such as *Bolbitis semicordata* and *B. virens*, the perine is not loose and it is folded into crowded, blunt, conical folds recalling the perine in some species of *Elaphoglossum*. In still others, such as *Bolbitis acrostichoides*, *B. crispatula* and *B. presliana*, the perine is adherent to the exine and almost devoid of folds. Fresh spores of all genera contain many large pale green plastids and small oil globules.

#### DISCUSSION

From a phylogenetic point of view, the Lomariopsidaceae have long been problematical. Most pteridologists consider them to be probably of aspidiaceous affinity: Christensen (1938) and Ching (1940) regard them as acrostichoid derivatives of the Dryopteroid ferns; Bower (1928) postulates affinity to the Thelypteridioid group, and Copeland (1947) to the Polystichioid group. Holttum (1947) suggests a derivation of the family from the Dennstaedtioid stock along with the Davalliaceae. All these hypotheses assume that the Lomariopsidaceae are evolved from free-veined ancestors, and a reticulate venation as in *Bolbitis* and *Lomagrumma* is evolved within the group. It is also often assumed that a two-ranked leaf arrangement and a solenostelic vascular cylinder of the rhizome represent the comparatively more primitive condition from which a multi-ranked leaf arrangement and a dictyostelic vascular cylinder is evolved, by the interpolation of extra rows of leaves between the original two rows. Because of its free veins and discrete sori, *Thysanosoria* is then regarded as representing the most primitive condition in the family. Recently, as the result of a detailed study of the sporophytes and gametophytes of several species of *Bolbitis* and *Egenolfia*, Nayar and Kaur (1965*b*) concluded that the species of *Bolbitis* which possess a complicated reticulate venation, many rows of leaves on the rhizome and a nearly dictyostelic vascular cylinder are possibly the more primitive; those with a simple venation pattern, a two-ranked leaf arrangement and a solenostelic vascular cylinder, as in most species of *Egenolfia*, are derived.



As described in this paper, the fertile pinnae of all genera, except *Egenolfia*, *Elaphoglossum* and *Thysanosoria*, possess a reticulate venation, even though the broad sterile pinnae of most of them have free veins. Since reproductive organs are generally more conservative in evolution, reticulate venation is probably the ancestral condition in the family; those genera such as *Bolbitis* and *Lomagrumma* are therefore comparatively more primitive in the family, whereas *Egenolfia* and *Thysanosoria* are not so primitive. The geographic ranges of the various genera probably give an indication of the relative age of the genera. The monotypic *Thysanosoria* with its very restricted geographic range can hardly be regarded as an old genus from which the others are evolved. On the other hand, the large genus *Bolbitis*, which is spread round the world, is more likely to be the older genus, while *Arthrobotrya*, *Egenolfia* and *Teratophyllum* are comparatively more recent. This again supports the possibility that *Bolbitis* is the more primitive genus in the group. In all probability, the ancestral condition in the family is one which has an elongated creeping rhizome, a dictyostelic vascular cylinder, many rows of leaves around the rhizome and a reticulate venation of the lamina. Taken in conjunction with cytology and spore morphology (Nayar and Devi, 1964; Nayar and Kaur, 1965c), this points to ferns like those of the Tectarioid group. The tendency towards the development of a free venation (through a goniopteroid pattern as in *Bolbitis*) as well as for the reduction of the fertile lamina, loss of indusium and development of acrostichoid condition, are manifest in the Tectarioid group, in genera such as *Pleocnemis*. An indication of the possible origin of a dorsiventral solenostele of the rhizome is found in some species of *Tectaria* in which some of the leaves on the ventral side of the procumbent or creeping rhizome are partially suppressed; they remain dormant and are associated with markedly smaller leaf gaps in the stelar cylinder of the rhizome (Nayar, unpublished data). Also, the leaves of some species of *Tectaria* possess associated roots, the root trace originating from the abaxial end of the leaf gap, recalling the leaf-associated roots of *Bolbitis*, *Egenolfia* and *Elaphoglossum* (Nayar and Kaur, 1965a; Bell, 1951a).

From the evolutionary point of view, *Bolbitis* possibly is the more primitive genus in the family. It exhibits a tendency towards evolution of high climbing forms with special venation to supply sporangia in the fertile leaves (*B. subsimplex*); this might lead on to the high climbing genera, as well as towards forms with a short, creeping, dorsiventral rhizome with simplification of venation pattern, leading to genera like *Egenolfia*. A tendency towards the development of a reticulate perine from a granulose one (through rugulose types as in *B. presliana*) is manifest in both the lines of specialization.

The presence of a set of special veins to supply the needs of the sporangia in the fertile pinnae of *Teratophyllum* was reported by Holttum (1954), and he rightly inferred that a similar condition may be found in some of the related ferns as well. The special venation, as found in most members of the Lomariopsidaceae, appears to be a special adaptation to specific environmental conditions. It is well developed in the high climbing species which have profuse acrostichoid distribution of sporangia. In genera like *Bolbitis*, which includes species with high climbing rhizomes as well as those with short, creeping rhizomes, a special venation is found only in the former. However, traces of a special venation occur in some others, like *B. presliana* and some species of *Egenolfia*, both of which possess a short, creeping rhizome. On the other hand, some of the high climbing, broad-leaved species of *Lomariopsis* and *Teratophyllum* lack any special veins while their sister species possess elaborate special veins. The degree of reduction of the fertile pinna does not seem to have any direct correlation to the presence or absence of a special venation. The development of water storing tissues in the leaf, hydathodes

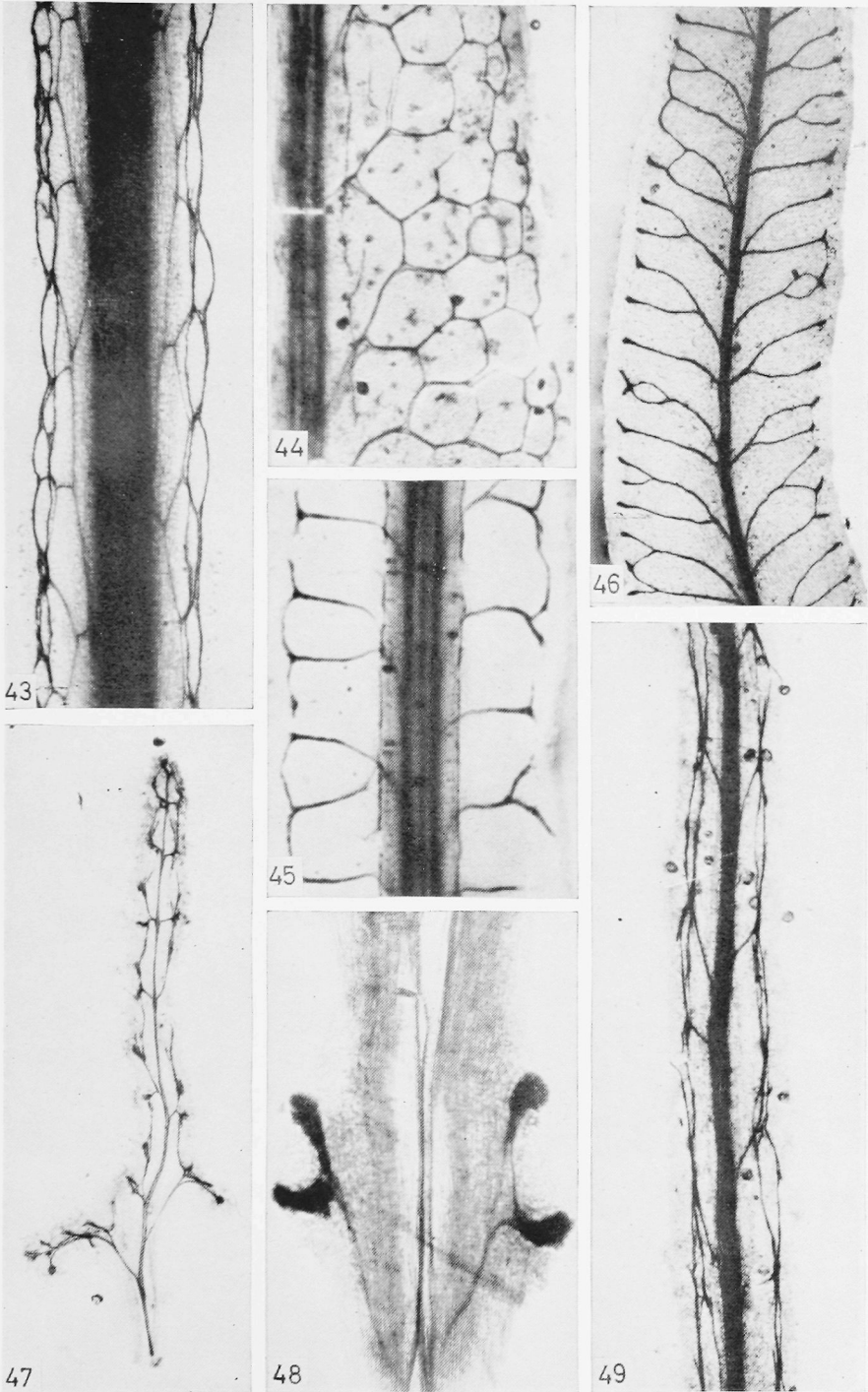
and special veins, are possibly adaptations developed by the Lomariopsidoid genera independently in response to the partial xerophytic conditions either of a rocky environment where some of the species with short rhizome grow, or induced due to the extremely elongated climbing nature of the rhizome which exposes the leaves to the wind and sun above the canopy of the tropical forests.

## ACKNOWLEDGMENTS

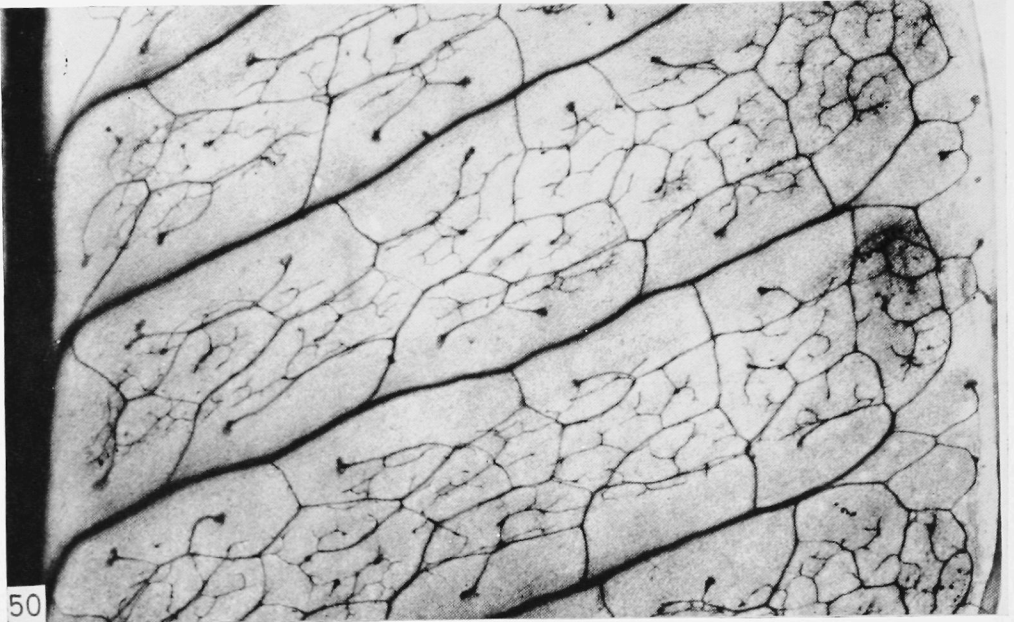
It is a pleasure to record here my gratitude to Professor R. E. Holttum, who suggested this problem to me and supplied most of the material used in this study. To Dr. Guido Moggi of the Florence University I am indebted for the supply of some fertile material of *Thyanosoria* from the Beccari collection. I am grateful to Professor K. N. Kaul, Director, National Botanic Gardens, for laboratory facilities and encouragement, and to my colleague, Dr. Surjit Kaur, for her help during the course of this study.

## REFERENCES

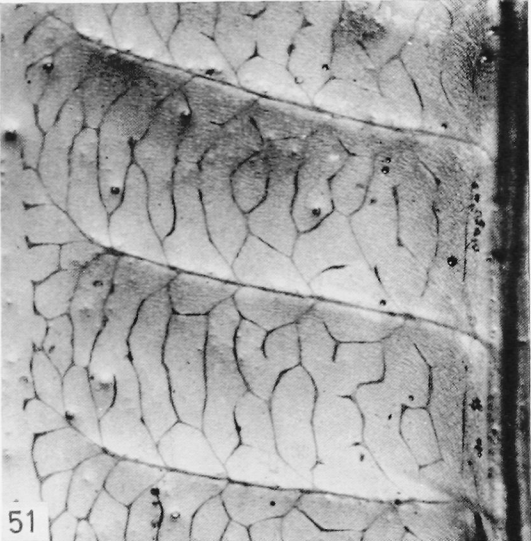
- BELL, P. R. (1950). Studies in the genus *Elaphoglossum* Schott. I. Stellar structure in relation to habit. *Ann. Bot.*, N.S., **14**, 545.
- BELL, P. R. (1951a). Studies in the genus *Elaphoglossum* Schott. II. The root and bud trace. *Ann. Bot.*, N.S., **15**, 333.
- BELL, P. R. (1951b). Studies in the genus *Elaphoglossum* Schott. III. Anatomy of the rhizome and frond. *Ann. Bot.*, N.S., **15**, 347.
- BOWER, F. O. (1928). *The Ferns*, Vol. III. Cambridge.
- CHING, R. C. (1940). On natural classification of the family Polypodiaceae. *Sunyatsenia*, **5**, 201.
- CHRISTENSEN, C. (1938). Filicineae; In Verdoorn's *Manual of Pteridology*. The Hague.
- COPELAND, E. B. (1928). *Leptochilus* and genera confused with it. *Philipp. J. Sci.*, **37**, 333.
- COPELAND, E. B. (1947). *Genera Filicum*. Waltham, Mass.
- ERDTMAN, G. (1952). *Pollen Morphology and Plant Taxonomy*. Uppsala.
- HOLTUM, R. E. (1937). Further notes on *Stenochlaena*, *Lomariopsis* and *Teratophyllum*. *Gdns' Bull. Straits Settl.*, **9**, 139.
- HOLTUM, R. E. (1938). A redefinition of the genus *Teratophyllum*. *Gdns' Bull. Straits Settl.*, **9**, 355.
- HOLTUM, R. E. (1947). A revised classification of leptosporangiate ferns. *J. Linn. Soc. (Bot.)*, **53**, 123.
- HOLTUM, R. E. (1954). *Flora of Malaya*, vol. II: *Ferns*. Singapore.
- NAYAR, B. K. (1964). Palynology of modern Pteridophyta. In Nair's *Advances in Palynology*. Lucknow.
- NAYAR, B. K. & DEVI, S. (1964). Spore morphology of Indian Ferns. I: Aspidiaceae. *Grana palynol.*, **5**, 83.
- NAYAR, B. K. & KAUR, S. (1964a). Ferns of India. XI. *Bolbitis*. *Bull. natn. bot. Gdns Lucknow*, No. **88**.
- NAYAR, B. K. & KAUR, S. (1964b). Ferns of India. XIII. *Egenolfia*. *Bull. natn. bot. Gdns Lucknow*, No. **100**.
- NAYAR, B. K. & KAUR, S. (1965a). Morphological studies on the fern genera *Bolbitis* and *Egenolfia*. I. The adult sporophyte of some species. *J. Linn. Soc. (Bot.)*, **59**, 127.
- NAYAR, B. K. & KAUR, S. (1965b). Morphological studies on the fern genera *Bolbitis* and *Egenolfia*. II. The gametophytes and juvenile sporophytes. *J. Linn. Soc. (Bot.)*, **59**, 141.
- NAYAR, B. K. & KAUR, S. (1965c). Spore morphology of the Lomariopsidaceae. *J. Palyn.*, **1**.
- STOKEY, A. G. & ATKINSON, L. R. (1957). The gametophyte of some American species of *Elaphoglossum* and *Rhipidopteris*. *Phytomorphology*, **7**, 275.



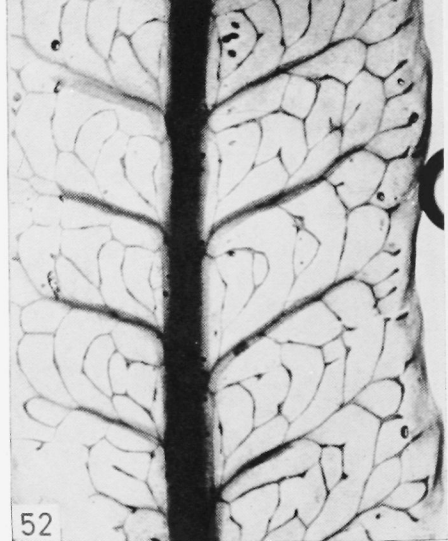
Figs. 43-49. Portions of the fertile pinnae of the Lomariopsidaceae, showing venation. 43. *Lomagramma sinuata* forma *papuana*. 44. *L. sinuata*. 45. *Lomariopsis spectabilis*. 46. *Teratophyllum arthropteroides*. 47. *Arthrobutyra articulata*. 48. *Egenolfia vivipara*. 49. *T. ludens*.



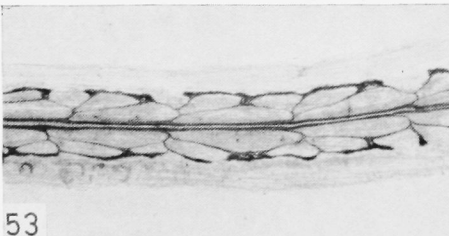
50



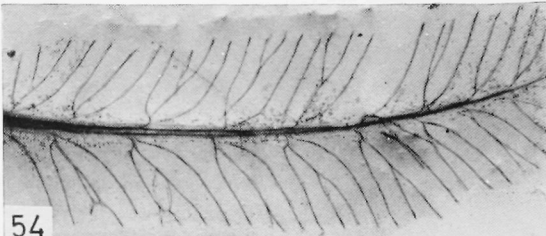
51



52



53



54

Figs. 50-54. Portions of the fertile pinnae of *Bolbitis* and *Egenolfia* showing venation. 50. *B. subsimplex*. 51. *B. heteroclita*. 52. *B. costata*. 53. *B. subcrenata*. 54. *E. sinensis*.

## APPENDIX

## Details of materials used in the study

Name of species	Locality	Collection No. and herbarium where specimen is located
1. <i>Arthrobotrya articulata</i> J. Sm. ( <i>Teratophyllum articulatum</i> Mett.)	N. Celebes Lake Lanao, Mindanao, Philippines	Koorders 17073; BO M. S. Clemens 1073; MICH
2. <i>Bolbitis costata</i> (Wall.) C. Chr.	Garo Hills, Assam, India	B. K. Nayar 50932; LWG
3. <i>B. crispatula</i> (Wall.) C. Chr.	Tura, Garo Hills, Assam, India	B. K. Nayar 63414; LWG
4. <i>B. heteroclita</i> (Pr.) Ching	Basistasram, Assam, India	P. Chandra 89090; LWG
5. <i>B. kanarensis</i> Nayar et Chandra	Castle Rock, Mysore, India	P. Chandra 95146; LWG
6. <i>B. presliana</i> (Fee) Ching	Agumbe, Mysore, India	P. Chandra 77712; LWG
7. <i>B. sculpturata</i> (Fee) Ching	Lushai Hills, Assam, India	P. Chandra 81152; LWG
8. <i>B. semicordata</i> (Moore) Ching	Jog Falls, Mysore, India	P. Chandra 77727; LWG
9. <i>B. subsimplex</i> (Fee) Ching	Tura, Garo Hills, Assam, India	B. K. Nayar 50931; LWG
10. <i>B. subcrenata</i> (Hook. et Grev.) Ching	Mercara, Coorg, India	B. K. Nayar 45553; LWG
11. <i>B. virens</i> (Wall.) Schott	Ponmudi, Kerala, India	B. K. Nayar 45058; LWG
12. <i>Egenolfia appendiculata</i> (Willd.) J. Sm.	Tura, Garo Hills, Assam, India	B. K. Nayar 50936; LWG
13. <i>E. asplenifolia</i> (Bory) Fee	Agumbe, Mysore, India	P. Chandra 77703; LWG
14. <i>E. bipinnatifida</i> J. Sm.	Haflang, N-Cachar Hills, Assam	P. Chandra 81103; LWG
15. <i>E. keralensis</i> Nayar et Kaur	Munnar, Kerala, India	P. Chandra 77752; LWG
16. <i>E. sinensis</i> (Baker) Maxon	Goalpara, Assam, India	B. K. Nayar 63446; LWG
17. <i>E. vivipara</i> (Hook.) C. Chr.	Garo Hills, Assam, India	B. K. Nayar 50928; LWG
18. <i>Elaphoglossum conforme</i> (Sw.) Schott	Shillong, Assam, India	B. K. Nayar 64508; LWG
19. <i>Lomagamma lomarioides</i> (Bl.) J.Sm.	G. Rasamala, Java, Indonesia	Raciborski, s.n.; BO
20. <i>L. perakensis</i> Beddome	Mt. Korinchi, Sumatra, Indonesia	Bunnemeijer 8711; L
21. <i>L. sinuata</i> C. Chr.	Cult., Hort. Bogor., Indonesia	Teysmann, s.n.; L
22. <i>L. sinuata</i> forma <i>papuana</i> C. Chr.	Idenburg River, New Guinea	Brass 13751; L
23. <i>L. sumatrana</i> v.A.v.R.	Sibolangit, N-Sumatra, Indonesia	Lorzing 12515; BO
24. <i>Lomariopsis cochinchinensis</i> Fee	Sungei Cheka, Pahang, Malaysia	Corner 24872; K
25. <i>L. kingii</i> (Copel.) Holttum	Eastern Highlands, New Guinea	L. J. Brass 32384; L
26. <i>L. intermedia</i> (Copel.) Holttum	Rossel Is., Eastern New Guinea	L. J. Brass 28475; L
27. <i>L. spectabilis</i> (Kze.) Mett.	S.E.-Java, Indonesia	H. O. Forbes, s.n.; L
28. <i>Teratophyllum arthropteroides</i> (Christ) Holttum	Los Banos, Luzon, Philippines	Elmer 18353; MICH
29. <i>T. gracile</i> (Bl.) Holttum	G. Beser near Tjidadap, Java	Backer 22674; BO
30. <i>T. ludens</i> (Fee) Holttum	Mandai Rd., Singapore, Malaysia	R. E. Holttum 24795; BO
31. <i>Thysanosoria dimorphophylla</i> Gepp. ( <i>Gymnogramma pteridiformis</i> Cesati)	Eastern New Guinea New Guinea	Mann, Type; K Beccari, Type; FI

This document is a scanned copy of a printed document. No warranty is given about the accuracy of the copy. Users should refer to the original published version of the material.