

COMPARATIVE MORPHOLOGY OF THE GAMETOPHYTE OF SOME THELYPTEROID FERNS

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ABSTRACT

A study of the development of the gametophytes of sixteen thelypteroid ferns reveals similarities and significant differences among them. Combinations of the diversified features of the prothalli appear to have a tremendous impact on identification and delimitation of the major taxa, and support the views of those authors who propose the taxonomic segregation of these ferns.

INTRODUCTION

The thelypteroid ferns comprising about one thousand species are chiefly inhabitants of the tropics and only a few of them occur in temperate regions. These plants are exceptionally varied in structure, yet they constitute a natural family, its members being easily distinguishable by their foliar acicular hairs, cauline scales with marginal and superficial appendages, and two hippocampus type of petiolar bundles. It is certainly significant that no other fern has this assemblage of vegetative characters. A critical survey through the literature reveals that probably in no other group of ferns the generic concept of the taxonomists is so highly contrasting as in the thelypteroids. Morton (1963) and Reed (1968) assembled all the thelypteroids in a single genus, *Thelypteris*. Iwatsuki (1964) on the other hand, subdivided them into three genera. Copeland (1947) recognised eight genera (including with them the unrelated *Currantia*) while Christensen (1938) tentatively suggested about twelve. Pichi Sermolli (1970) stated that no less than eighteen genera have to be kept distinct, and increased this number to thirtytwo in 1977 (Pichi Sermolli, 1977); Ching (1963) maintained nineteen genera in Asia. Holttum (1971), in his new system of genera in the Old World *Thelypteridaceae* circumscribed twentythree genera. Our knowledge of the morphology of the sporophytes of these plants is rapidly increasing due to the intensive studies of Prof. R. E. Holttum, but unfortunately only a small proportion of the total number of the thelypteroid fern species have had their gametophytes studies. This is certainly a pity, because the results so far obtained in prothallial studies of these plants are very encouraging, and have provided complementary evidence in the systematics of these plants (Momose, 1937–42; Stokey, 1960; Nayar and Chandra, 1963; Atkinson, 1971, 1975a, 1975b; Atkinson and Stokey, 1973; Mitra and Sen, 1969; and Holttum, Sen and Mitra, 1970).

The objectives of this paper are to describe the gametophytes of 16 species belonging to this group and to examine how far the features of this generation support the present day classification of these plants, based mainly on the characteristics of the sporophytes.

MATERIAL AND METHODS

Spores were obtained from different places and their sources are indicated below:

Species	Source
<i>Ampelopteris prolifera</i> (Retz.) Copel. (Type and sole species of the genus <i>Ampelopteris</i>)	Kalyani
<i>Christella parasitica</i> (L.) Lév. (Type species of the genus <i>Christella</i>)	Singapore
<i>Christella dentata</i> (Forssk.) Brownsey & Jermy	Kalyani
<i>Coryphopteris arthrotricha</i> Holttum	Cameron Highlands, Malaya
<i>Coryphopteris gymnopoda</i> (Baker) Holttum	Mt. Kinabalu, Sabah
<i>Cyclosorus gongyloides</i> (Schkuhr) Link (Type species of the genus <i>Cyclosorus</i>)	Sonarpur, West Bengal
<i>Metathelypteris dayi</i> (Bedd.) Holttum	Malaya
<i>Metathelypteris flaccida</i> (Bl.) Ching	Malaya
<i>Pneumatopteris ecallosa</i> (Holtt.) Holttum	Malaya
<i>Pneumatopteris glabra</i> (Copel.) Holttum (M. G. Price 529)	Philippines
<i>Pronephrium nudatum</i> (Roxb.) Holttum	Darjeeling
<i>Sphaerostephanos baramensis</i> (C. Chr. ex C. Chr. et Holtt.) Holttum ined.	Mt. Kinabalu, Sabah
<i>Sphaerostephanos confertus</i> (Brause) Holttum (Jermy 214/1970)	New Guinea
<i>Sphaerostephanos invisus</i> (Forst) Holttum (Jermy 8016)	New Guinea
<i>Sphaerostephanos penniger</i> (Mett.) Holttum	Malaya
<i>Thelypteris palustris</i> Schott. (Type species of the genus <i>Thelypteris</i>)	Holland

The type species of the genera *Ampelopteris*, *Christella*, *Cyclosorus* and *Thelypteris* have been deliberately included in the present study for such species determine the application of generic names and are used as standards against which the distinctive character combinations found in newly recognised species groups are judged. Where material of the type species of a genus under investigation was not available, at least two species of the taxon were investigated with the idea that the evidence obtained from more than one species of a genus would be stronger than that acquired from a single species. *Pronephrium*, as recognized by Holttum (1972), is a complex genus and is divided into three sections. *P. nudatum* (Roxb.) Holttum belongs to the section *Pronephrium* and is considered to be near to *P. lineatum* (Bl.) Presl, the type species of the genus.

Spores were sown on the pteridophytic medium (Kato, 1969) and also on Beneke's medium (with added $\text{Ca}(\text{NO}_3)_2 \cdot \text{H}_2\text{O}$ to promote growth especially during the early stages of development) solidified by 1% agar. Lighting was from artificial fluorescent light combined with 60 Watt white (f/40) for a 12 hour day. The temperature of the culture room was maintained at 22 ± 2 °C.

In the following statement, generic names are used for convenience, but naturally they refer only to the species here investigated.

OBSERVATIONS

Mature thelypteroid spores usually contain drops of oil and are apparently devoid of chloroplasts. The interval of time between sowing of spores of different taxa under investigation and their time of germination is illustrated in the accompanying histogram (Fig. 1). The spores of all the species with the exception of *Pronephrium nudatum*, *Coryphopteris arthrotricha*, and *C. gymnopoda* germinate within 3–8 days after sowing. There is an enlargement in the primary cell before the initiation of the first division, which usually cuts off the hyaline rhizoidal initial

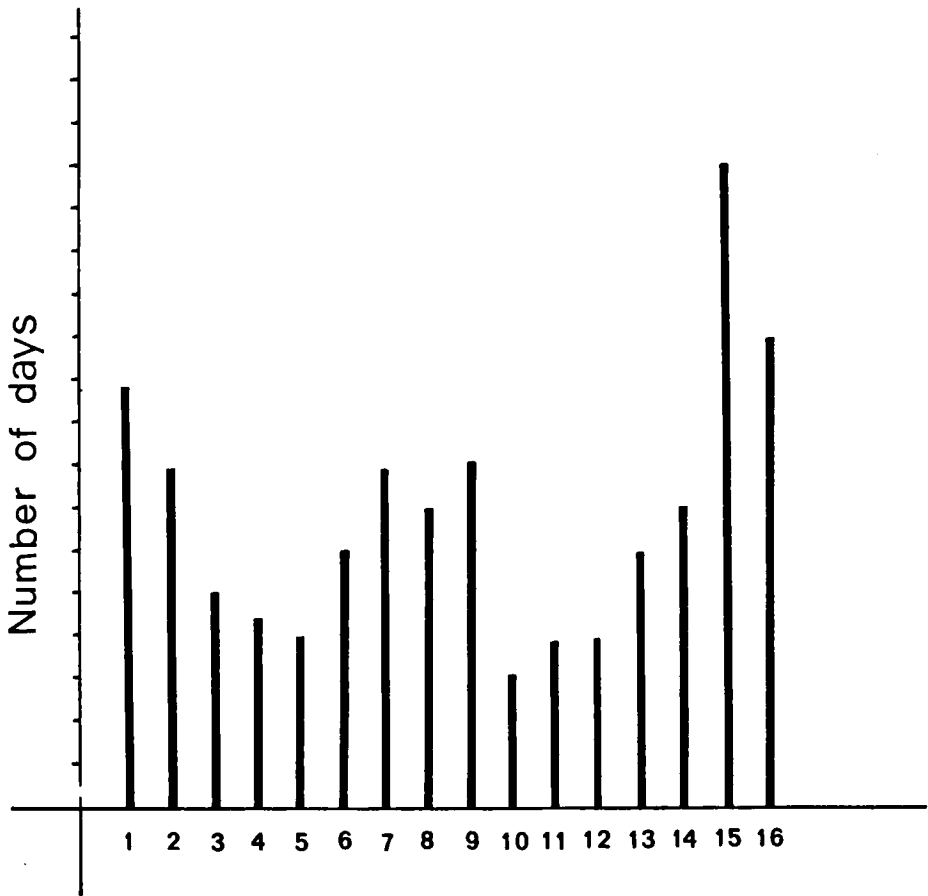


Fig. 1. Histogram illustrating the interval of time between sowing of spores of different species and their time of germination. 1 unit = 1 day.

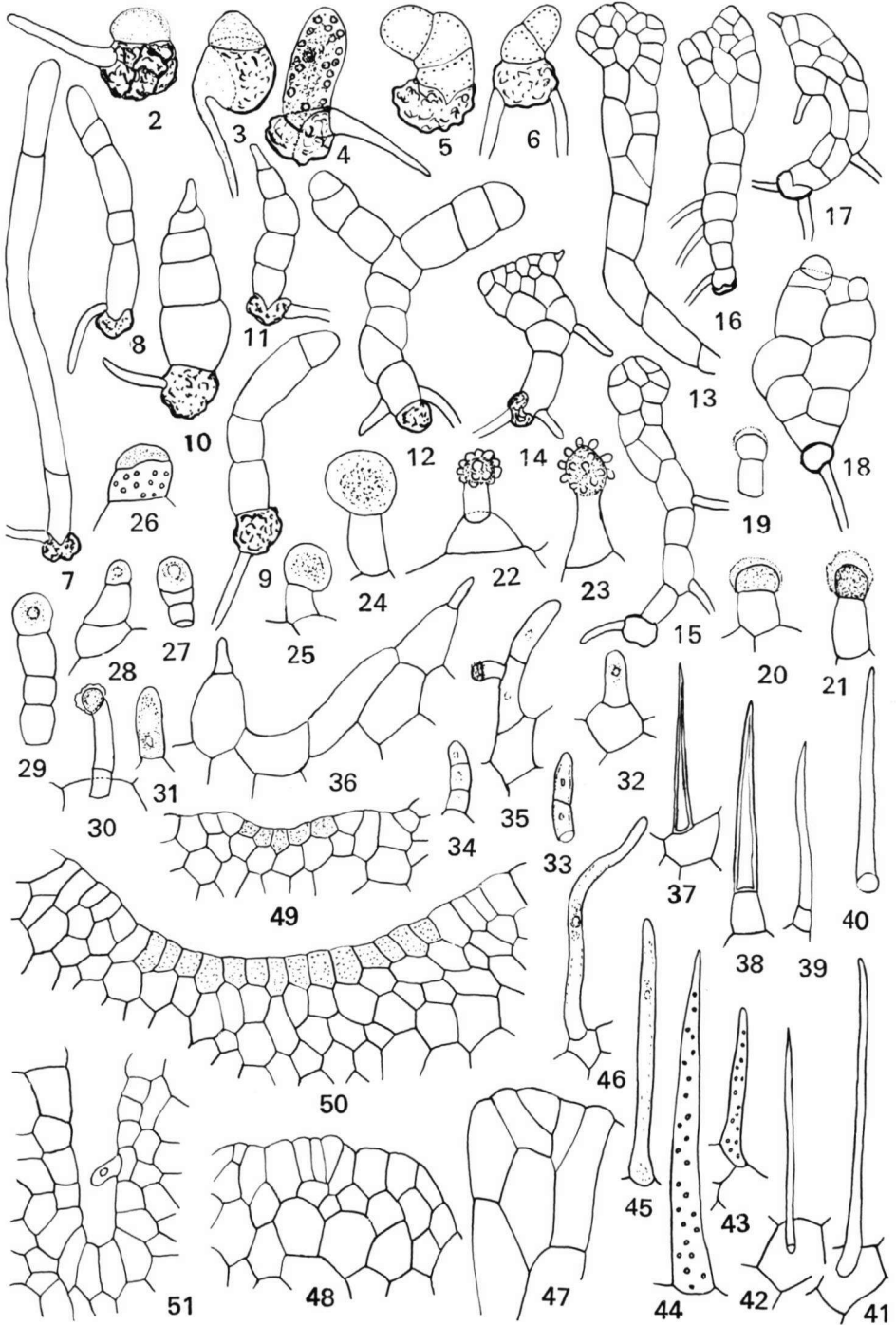
1. *Pronephrium nudatum*. — 2. *Sphaerostephanos confertus*. — 3. *Sphaerostephanos penniger*. — 4. *Sphaerostephanos invisus*. — 5. *Sphaerostephanos baramensis*. — 6. *Metathelypteris flaccida*. — 7. *Metathelypteris dayi*. — 8. *Christella dentate*. — 9. *Christella parasitica*. — 10. *Ampelopteris prolifera*. — 11. *Pneumatopteris glabra*. — 12. *Pneumatopteris ecallosa*. — 13. *Thelypteris palustris*. — 14. *Cyclosorus gongyloides*. — 15. *Coryphopteris arthrotricha*. — 16. *Coryphopteris gymnopoda*.

laterally by a wall parallel to the polar axis of the spore (Figs. 2 and 3). In none of the species the germination follows the *Vittaria* type, reported by Nayar (1971). The first prothallial cell is generally bright green and short except in *Pneumatopteris* and *Thelypteris* where occasionally it is elongate (Fig. 4). In some developing germ filaments, the rhizoid formation is delayed (Fig. 5), while in some others two or more rhizoids are produced by the primary rhizoidal cell (Fig. 6). The germ filaments are generally composed of cells almost of similar size and only occasionally in *Thelypteris* and *Metathelypteris* they are constituted of short and long cells (Figs. 8 and 9). In *Coryphopteris* the cells constituting the germ filaments are conspicuously rectangular to squarish in outline. The germ filaments in this genus are often branched and usually terminate into a papillate hair (Figs. 10 and 12). Similarly, the terminal growth of the germ filaments in *Cyclosorus gongylodes* may occasionally though not always be stopped by the differentiation of the tip cell into a papilla (Fig. 11). Interestingly in crowded cultures the cells of the germ filaments become narrow and elongate (Fig. 7). The basal cell of the germ filaments is usually short, barrel shaped and is packed with chloroplasts.

The cell walls dividing the germ filament are almost always transverse, but in *Pneumatopteris* and *Coryphopteris* they are sometimes oblique (Figs. 5, 6 and 13). Vertical division in the terminal cell or in any median cell of the filament initiates plate formation. In *Metathelypteris*, *Pronephrium*, *Pneumatopteris*, and *Sphaerostephanos* only a few distal cells of the germ filament are involved in cell plate formation (Figs. 13, 14, 15, and 16), but in *Thelypteris*, *Ampelopteris*, and *Cyclosorus* most of the cells of the filament except the basal cell or a few proximal ones undergo division to form a cell plate (Figs. 17 and 18). The early stages of cell-plate formation are brought about by initiation of vertical cell wall formation usually in 5–15 days old prothallial filaments. In *Coryphopteris gymnopoda* and *Pneumatopteris ecallosa*, however, initiation of such vertical divisions in the prothallial filaments are delayed and the cell walls do not appear until the filaments are 20–25 days old. Interestingly in *Ampelopteris* and *Sphaerostephanos* the germ filaments begin to form plates even from the fourth day from the date of their germination.

Hairs usually begin to develop on prothalli almost simultaneously with the initiation of the apical meristem. In *Coryphopteris*, *Cyclosorus*, and *Pneumatopteris* they, however, begin their appearance early in the ontogeny of the gametophytes.

Plate I. Figs. 2–51. — Figs. 2, 5, and 7, *Coryphopteris gymnopoda*. Figs. 3, 28, 36 and 49, *Christella dentata*. Figs. 4, 9, 18, 26, and 41, *Thelypteris palustris*. Figs. 6, 13, 25, 40 and 48, *Pneumatopteris glabra*. Fig. 8, *Metathelypteris daii*. Figs. 10, 12, 20, 24, 45 and 50, *Coryphopteris arthrotricha*. Figs. 11, 32, 39 and 46, *Cyclosorus gongylodes*. Fig. 14, *Pneumatopteris ecallosa*. Figs. 15, 21, 29 and 38, *Metathelypteris flaccida*. Figs. 16, 23, 43, 44 and 51, *Pronephrium nudatum*. Fig. 17, *Ampelopteris prolofera*. Figs. 19, 22, 30, 42 and 47, *Sphaerostephanos penniger*. Figs. 27, 31, 33 and 35, *Sphaerostephanos confertus*. Fig. 34, *Sphaerostephanos invisus*. Fig. 37, *Christella parasitica*. 2–4, development of first prothallial cell and the first rhizoidal cell. 5, germ filament without any rhizoid. 6, basal cell with two rhizoids. 7, narrowly elongated germ filament in crowded culture. 8 and 9, germ filament with cells of different sizes. 10 and 11, germ filament ending with papillate hair. 12, branched germ filament. 13–18, different types of cell-plate formation. 19–30, different types of glandular hairs. 33 and 34, simple multicellular hairs. 35, branched multicellular hair. 36, papillate hairs on extended cells. 37–44, different types of acicular hairs. 45 and 46, long flexuous hairs. 47–49, single and multicellular apical meristematic cells. 50, shallow apical notch. 51, narrow apical notch. 2, 5, 6, 8–10, 13, 30, 33–37, 39–46, 48, 50, 51, $\times 150$; 3, 4, 19–25, 27–29, 31, 32, 38, 47, 49, $\times 300$; 7, 11, 12, 14–18, $\times 90$; 26, $\times 640$.



The prothalli of *Sphaerostephanos*, *Thelypteris*, and *Metathelypteris*, on the other hand, remain naked until the antheridial initials are differentiated. Mature prothalli of all the species are heavily clothed with simple (Figs. 31 and 32) and glandular hairs, both at their margin and on the surface. Most of the glandular hairs secrete an extracellular cap. The outer surface of these extracellular caps may be smooth in some species of *Sphaerostephanos* and *Coryphopteris* (Figs. 19 and 20), or irregular or warty in *Metathelypteris*, *Sphaerostephanos penniger*, and *Pronephrium nudatum* (Figs. 21, 22 and 23). Significantly, a few glandular hairs without any extracellular cap occur close to the midrib of prothalli of *Coryphopteris* and *Pneumatopteris* (Figs. 24 and 25). In *Thelypteris* the glandular hairs may be very short and thick (Fig. 26), but in *Sphaerostephanos*, *Christella*, and *Metathelypteris* they are long and multicellular (Figs. 27, 28 and 29). The multicellular glandular hairs of *Sphaerostephanos penniger* are conspicuously slender (Fig. 30). *Sphaerostephanos* characteristically bears multicellular simple hairs (Figs. 33 and 34) intermixed with multicellular branched glandular hairs (Fig. 35). Occasionally both in *Sphaerostephanos* and *Coryphopteris* these hairs are borne on raised prothallial cells (Figs. 22 and 23), but in *Christella dentata* the hairs are often borne on extended cells of the ragged prothallial margin (Fig. 36). Acicular hairs which occur invariably in all the thelypteroids, are usually late in development and may not appear until archegonia are differentiated. In *Cyclosorus*, *Thelypteris*, and *Coryphopteris* often these hairs appear only in very old prothalli. Probably for this reason Holttum, Sen, and Mittra (1970) and Atkinson and Stokey (1973) failed to see these hairs in *Cyclosorus*. Probably for the same reason Holttum, Sen and Mittra (1970) could not find acicular hairs on the prothalli of *Thelypteris* studied by them. Often the gametophytes of *Coryphopteris* are without acicular hairs for the first two years after their germination. The acicular hairs are without any chloroplasts and usually grow at the anterior margin of the prothalli and on either side of the midrib. In *Christella* and *Metathelypteris* the acicular hairs are 1–3 celled, thick-walled, stiff and have dark brown pointed apices (Figs. 37 and 38). In addition to the acicular hairs, 1- to 2-celled chlorophyllous acicular hairs with hyaline walls occur in *Christella*, *Ampelopteris*, *Cyclosorus*, *Sphaerostephanos*, *Pneumatopteris*, and *Thelypteris* (Figs. 39 and 40). Sometimes in *Thelypteris* and *Sphaerostephanos* some of these chlorophyllous hairs become narrow and elongate (Figs. 41 and 42). The tips of the chlorophyllous hairs are usually sharply pointed, but in *Pronephrium* these are rather blunt (Figs. 43 and 44). The chlorophyllous hairs in *Pronephrium* are characteristically packed with minute chloroplasts. Some of the glandular hairs in *Coryphopteris* become conspicuously yellow at maturity. Long, unicellular flexuous hairs characteristically occur at the anterior margin of the prothalli of *Coryphopteris* and *Cyclosorus* (Figs. 45 and 46). Atkinson (1975b) reported the occurrence of similar 'conspicuously elongated marginal cells' in *Coryphopteris* sp.

The rhizoidal initials contain a few sparsely distributed small chloroplasts, which degenerate along with their elongation. Mature rhizoids are long, flexuous, and hyaline. They are generally unicellular and only occasionally they possess a basal septum. Initiation of rhizoids is often delayed until the germ filaments form cell plates. The rhizoids are negatively phototropic but their initiation is not influenced by gravity. Prothalli in culture lighted from beneath produce rhizoids both on the dorsal and ventral surfaces. A mature prothallus bears numerous rhizoids entangled with each other. These rhizoids are usually restricted to the ventral surface mostly on the midrib region and only occasionally a few of them occur on

either side of the midrib. Interestingly, in *Metathelypteris* and *Cyclosorus* some of the rhizoids become reddish brown at maturity. In *Coryphopteris* the rhizoids are stiff, short, and pale on the anterior part of the prothalli, but stunted and brown in the posterior region. Atkinson (1975b) also noted similar rhizoids in this genus. Forking of the rhizoids is a common feature in all these genera.

An apical meristematic cell is formed by oblique divisions in the terminal cell of a germ filament. Immediately after the establishment of the apical cell, flattening of the prothallus proceeds by the active divisions of this meristematic cell. In *Cyclosorus* and *Sphaerostephanos* the apical meristematic cell is distinct (Fig. 47), while in *Pneumatopteris* it is quickly replaced by a meristematic tissue (Fig. 48). The apical cell stage is omitted in *Christella*, where the meristematic activity is due to a group of cells (Fig. 49). The apex of the thallus at the region of the meristematic cell becomes notched and later cordate. This notch is deep in *Christella*, *Pronephrium*, *Thelypteris*, *Metathelypteris*, and *Pneumatopteris* (Fig. 51) but in others it is broad and shallow (Fig. 50). The developing prothalli in *Pneumatopteris*, *Thelypteris*, and *Metathelypteris* become asymmetrical due to the shifting of the apical meristem to a side. In the species investigated the two prothallial wings usually do not overlap each other excepting in *Thelypteris* and *Pneumatopteris* where the wings overlap slightly. Due to unfavourable conditions of illumination or food supply, growth in developing gametophytes of all the species studied becomes arrested and the germ filaments or even the cell plates fail to differentiate apical meristematic cell or tissue. Such gametophytes without apical meristematic cell or tissue generally become an irregular plate (Fig. 52), and occasionally form sex organs, which without any exception are always antheridia (Fig. 53).

The prothalli, especially at old age, in all the genera, are capable of producing small thalli for vegetative propagation. In *Ampelopteris*, *Pneumatopteris*, *Thelypteris*, *Sphaerostephanos*, and *Christella* the small propagative prothalli originate from a marginal or superficial cell of the prothalli (Figs. 54 and 55). Formation of juvenile prothalli from proliferated cells of the midrib is a common feature in *Metathelypteris*. *Sphaerostephanos* with branching prothalli reproduces vegetatively by the progressive death of the old parts, reaching the point of branching, and the two surviving branches continuing growth as two separate plants.

In ripe young age the prothallial midrib of *Christella*, *Cyclosorus*, *Thelypteris*, *Metathelypteris*, *Ampelopteris*, and *Pronephrium* is short, round and strong (Fig. 57), but in old age it undergoes a considerable change in its aspect. In *Pneumatopteris* the midrib is rather less developed, short, broad and the wings are not sharply distinct from the midrib (Fig. 58). In this genus the midrib ends much below the apical notch and is about 4–5 cells thick at its central region. The region around a developing embryo, however, becomes active, forms small and large hexagonal cells about 15 or more cells in thickness. In the remaining genera, excepting in *Sphaerostephanos* and *Coryphopteris*, the midrib in old thalli becomes very heavy, round and extends the entire length of the gametophyte.

The midrib in *Metathelypteris* is very strong (Fig. 59), composed of large hexagonal cells, and its limiting cells are well arranged, narrow, and elongate. It is usually 6–8 or even 10 cells thick and 20–25 cells broad. At maturity it becomes brownish, swollen ventrally, and bears zygotes all along its length. The wings around the midrib at the apical region of the gametophyte of this genus often undergo degeneration and the cells of the midrib proliferate to produce many small

prothalli. Interestingly the midrib in this genus extends beyond the apical notch as a stout column similar to that of the prothallus of *Cibotium barometz* (Sen and Sen, 1979).

In *Sphaerostephanos* and *Coryphopteris* the midrib is narrow but strong. In both these genera it is extended throughout the entire length of the prothallus from the very young age (Figs. 60–63). The midrib is 4–5 cells thick and is composed of uniformly hexagonal cells in *Sphaerostephanos*, while in *Coryphopteris* it is 8 cells thick and its mass of hexagonal cells is limited on either side by a layer of elongated cells. The rate of prothallial development is variable in different genera. It is very slow in *Metathelypteris*, *Thelypteris*, and *Sphaerostephanos*, while in *Pronephrium* and in the remaining genera it is very rapid.

The ripe young prothalli are broadly cordate to almost reniform in *Christella*, *Cyclosorus*, *Metathelypteris*, and *Thelypteris* (Fig. 57) and cordate in *Pronephrium*, *Coryphopteris*, and *Ampelopteris* (Fig. 59 and 60). In *Sphaerostephanos* as well the thalli are cordate but they have a long tapered base from the very early age (Figs. 61–63) and a very wide and shallow apical notch. The margin of the large wings of *Coryphopteris* is entire while in *Sphaerostephanos* it is very ruffled.

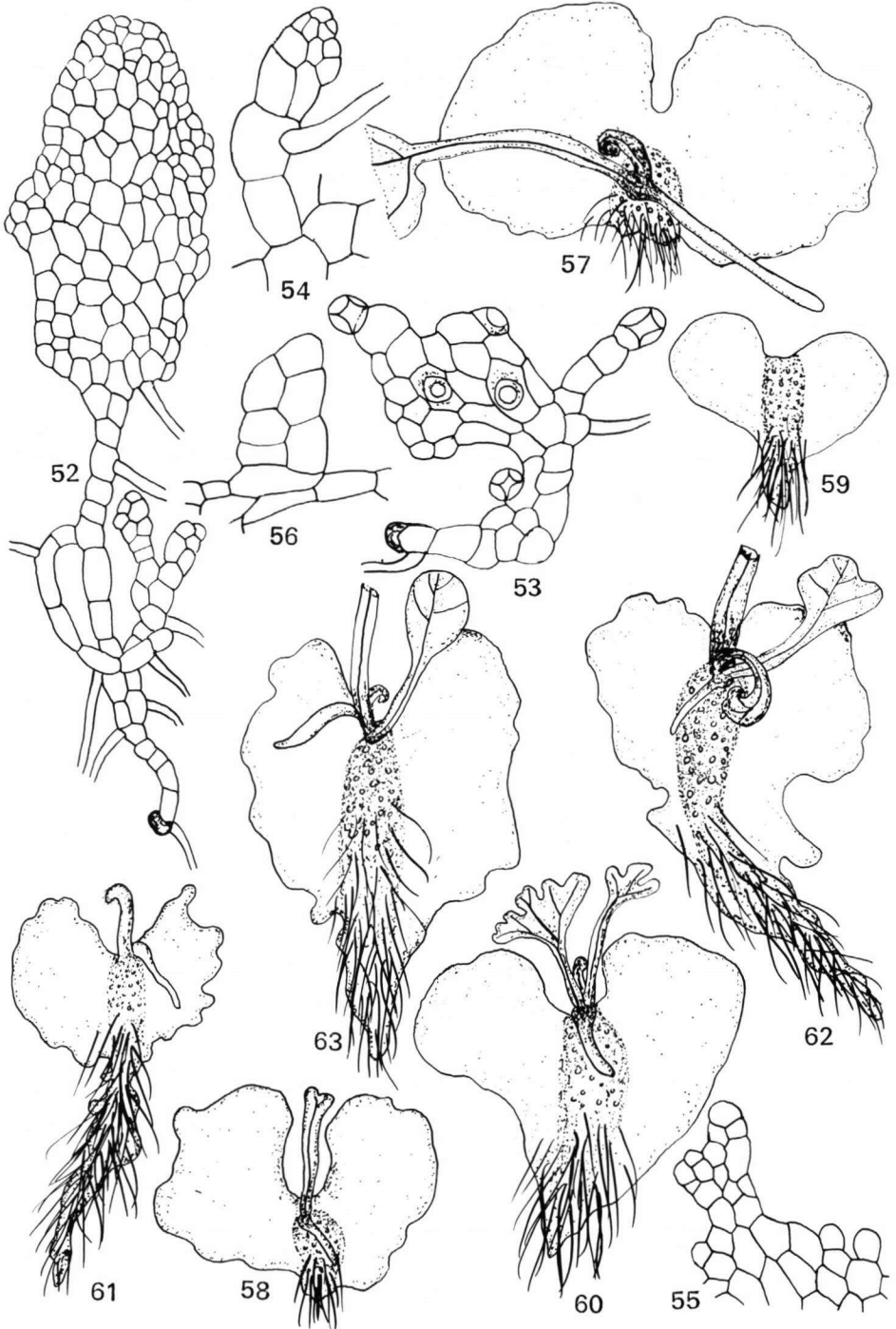
Old thalli of *Metathelypteris*, *Christella*, and *Ampelopteris* are irregularly circular along with their spreading wings (Figs. 64 and 66) while those of *Thelypteris*, *Cyclosorus*, and *Pronephrium* are typically reniform with sinuous or flat bases (Figs. 65, 67 and 68). In *Thelypteris* ultimately the thalli become asymmetrical. The apical notch in old prothalli of *Cyclosorus*, *Christella*, and *Pronephrium* is usually broad but due to prolonged culture it may become irregularly lobed (Figs. 66 and 67). Mature prothallial wings of *Cyclosorus* are sinuous and uplifted, and never ragged at the margin. In this genus proliferation of cells at the apical region occurs in such a way that many prothalli remain joined end to end. The prothallial margin in *Metathelypteris*, *Pronephrium*, and *Ampelopteris* similar to that of *Cyclosorus* is entire and slightly sinuous but never uplifted.

Old thalli of *Metathelypteris* are large and stout (Fig. 64) while those of *Pneumatopteris* are small and have almost flat or little downwardly projecting bases (Figs. 58 and 69). The wings of *Pronephrium* are projected around the wide and deep apical notch.

The cells of the wings in all the taxa are usually uniformly thin-walled and densely chlorophyllous. Occasionally, however, the cellwalls become thickened at corners or along the sides. Such collenchyma-like thickenings occur in *Pronephrium*, *Ampelopteris*, *Christella*, and *Cyclosorus* (Figs. 70–73). They are lacking in *Sphaerostephanos*, *Pneumatopteris*, and *Metathelypteris*. In *Christella* and *Ampelopteris* these thickenings are often projected and peg-like in appearance.

Antheridia begin to appear in young cell-plates even before the initiation of the apical meristematic cell. They may be marginal, superficial, or even occur on extensions of the prothallial plates near the base. Full grown prothallia seldom bear

Plate II. Figs. 52–63. — Figs. 52 and 60, *Coryphopteris arthrotricha*. Fig. 53, *Ampelopteris prolifera*. Fig. 54, *Sphaerostephanos baramensis*. Fig. 55, *Pneumatopteris ecallosa*. Fig. 56, *Metathelypteris flaccida*. Fig. 57, *Christella dentata*. Fig. 58, *Pneumatopteris glabra*. Fig. 59, *Pronephrium nudatum*. Fig. 61, *Sphaerostephanos invisus*. Fig. 62, *Sphaerostephanos confertus*. 52 and 53, meristematic cell-plate. 54–56, small propagative thalli. 57–63, mature prothalli. 52, $\times 90$; 53, $\times 50$; 54–56, $\times 150$; 57–63, $\times 7$.



antheridia. In *Christella* and *Metathelypteris* the antheridia are generally restricted to the midrib region (Fig. 74), while in *Cyclosorus*, *Pronephrium*, and *Ampelopteris* they are scattered on the wings. In the remaining genera a large number of antheridia occur at the margin and only a few develop on the prothallial surface. Occasionally antheridia occur in a row or in a group (Figs. 75–77). Antheridia in *Pneumatopteris* and *Metathelypteris* are stalked, but in the remaining genera they are sessile and usually globose (Figs. 79–81). In crowded cultures or under unfavourable conditions of growth, the thalli continue to produce antheridia for an indefinite period. During early stages of development antheridia contain numerous chloroplasts, most of which, except in *Christella* and *Pronephrium*, undergo degeneration. Mature antheridia of *Christella* remain packed with chloroplasts.

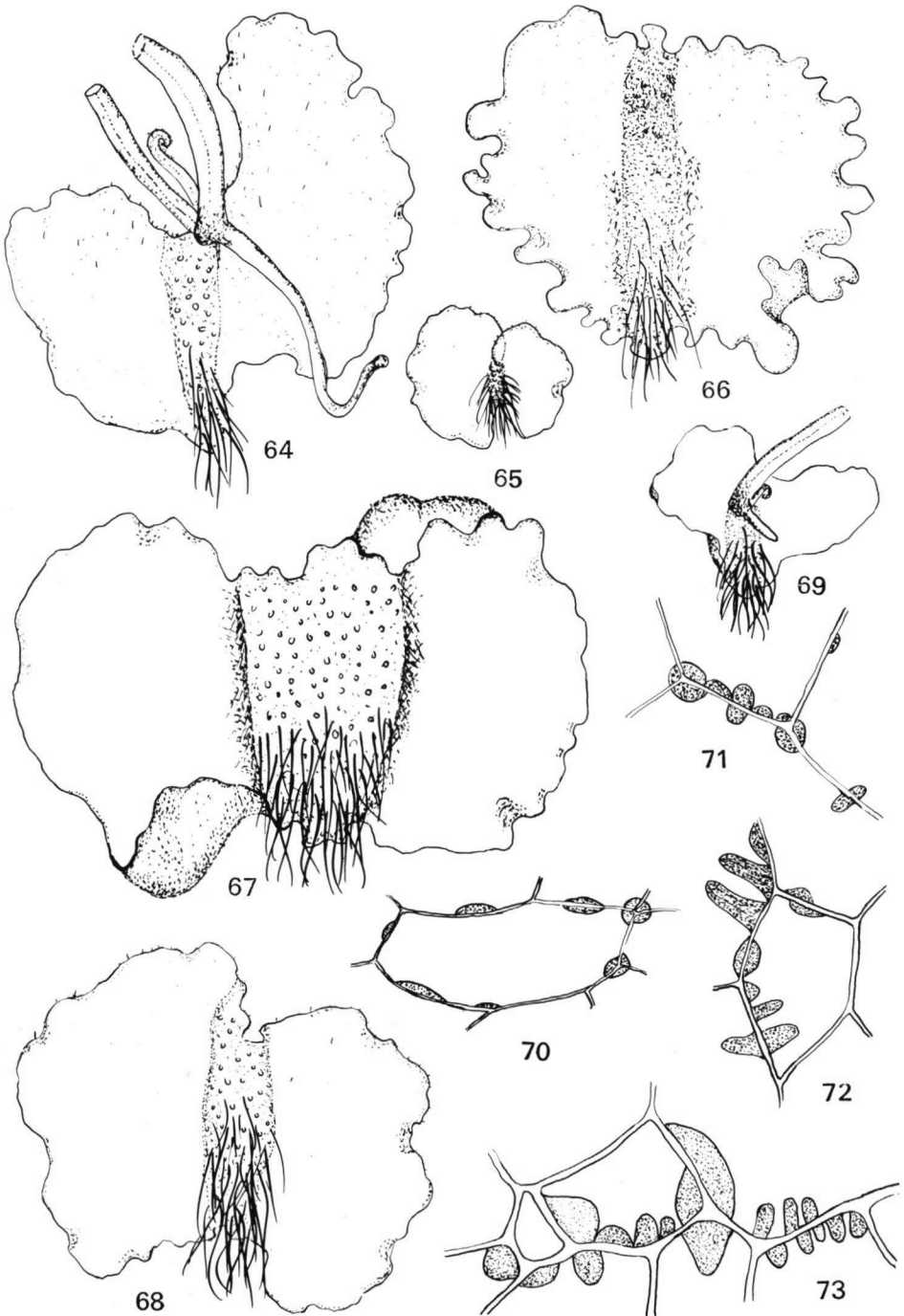
An antheridial initial at first cuts off its basal cell and then the cap cell. The cap cell is large, and it becomes 2-celled in *Thelypteris*, *Pneumatopteris*, *Christella*, and *Sphaerostephanos* (Fig. 82). In *Coryphopteris*, *Sphaerostephanos*, *Thelypteris*, *Metathelypteris*, and *Pneumatopteris* it is sloughed off making way for the antherozoids to escape (Fig. 83), while in *Cyclosorus* and *Christella* the one or two celled cap remains attached to the antheridium at one point even after the formation of the antheridial opening and later collapses (Fig. 80 and 81). The basal cell is usually funnel-shaped. But it is disk-shaped in *Coryphopteris* (Fig. 84) and elongate and pendulous in *Metathelypteris*, *Sphaerostephanos* and *Pneumatopteris* (Fig. 85).

Archaeogonial initials begin to develop from the derivatives of the apical meristem simultaneously with the initiation of the prothallial midrib. Usually the archaeogonia occur on the lower surface of the thalli. But prothalli receiving light on both the surfaces under cultural condition develop archaeogonia both on the upper and the lower surface. The archaeogonial neck in all the genera is short, stout, bulbous, slightly curved at the tip, 3–4 cells in height, and almost oval in optical section (Figs. 86–88). The canal cells are broad except in *Pneumatopteris*, *Thelypteris*, and *Metathelypteris* where they are comparatively narrow (Figs. 89 and 90). There is a well arranged nutritive layer around the developing zygote in *Pronephrium*, *Cyclosorus*, and *Pneumatopteris* (Fig. 91). Apogamy has only been observed in *Pronephrium nudatum* (Fig. 92).

DISCUSSION

The gametophytes of thelypteroid taxa examined in this study are superficially alike in having cordate thalli, marginal and superficial hairs, abundant rhizoids, and sex organs of the advanced type. But if one examines the detailed aspects of the prothalli, hairs, apical meristematic region, the rhizoids, and the position of the sex organs of the major taxa one finds the superficial similarity hiding a great diversity. Significantly, combinations of some of these diversified features appear to have tremendous impact in identifying and delimiting a taxon. For example, the gametophytes of *Coryphopteris* are characterised by yellow glandular hairs, two

Plate III. Figs. 64–73. — Fig. 64, *Metathelypteris flaccida*. Fig. 65, *Thelypteris palustris*. Fig. 66, *Christella dentata*. Figs. 67 and 70, *Cyclosorus gongyloides*. Figs. 68 and 71, *Pronephrium nudatum*. Fig. 69, *Pneumatopteris ecallosa*. Fig. 72, *Ampelopteris prolifera*. Fig. 73, *Christella parasitica*. 64–69, mature prothalli after prolonged culture. 70–73, collenchyma-like thickenings on cell walls. 64–69, $\times 7$; 70, 72, 73, $\times 300$; 71, $\times 435$.



types of rhizoids (e.g. stiff, short and pale, and stunted and brown), and the papillate hairs terminating most of the germ filaments. Occurrence of long flexuous hairs is also another characteristic of the genus. Moreover the frequent occurrence of two embryos on a prothallus indicate primitiveness of the genus. Spores with folded perine forming partial reticulum is another constant gametophytic feature of the genus *Coryphopteris*.

Metathelypteris and *Christella* both have large circular prothalli and acicular hairs with reddish brown tips. These reddish brown hairs are very distinct from the robust multicellular structures with a red terminal cell found in *Chingia pseudoferox* (Atkinson, 1975a). The young thalli of *Metathelypteris* and *Christella* are broad and have flat bases and uplifted wings. They develop antheridia only at the central midrib region. *Metathelypteris* can easily be distinguished from *Christella* by the features of their midrib. The midrib of *Metathelypteris* is very strong and it extends beyond the apical notch. The central cushion consists of large hexagonal cells delimited on either side by two layers of narrow elongated cells. In *Christella* the midrib never extends out of the apical region and is composed of only hexagonal cells, the narrow elongated cells on either side of the midrib being absent. In addition to these, hyaline, short acicular hairs, multicellular glandular hairs and pegged collenchyma-like outgrowths on the prothallial walls characterise *Christella*. The sporoderm of *Christella* is winged and its exine bears baculae and spines intermixed with a few verrucae. In *Metathelypteris* on the other hand, the sporoderm is partially reticulate and the exine is smooth or little granulate.

Long flexuous hairs intermixed with small acicular hairs, and peg-like outgrowths of very various forms on the walls of the wingcells characterise *Cyclosorus*. Most of the germ filaments in this genus, similar to those of *Coryphopteris*, end in a papillate hair. Sporoderm of *Cyclosorus* is characteristically wrinkled, partially reticulate, and bears a few spines and verrucae on its exine.

In *Sphaerostephanos* the cordate thalli have very much elongate bases tapered downwards. Simple multicellular hairs which develop only in the members of this genus, occur in association with hyaline acicular hairs and multicellular glandular hairs. The gametophytes of the species *invisus*, which has recently been placed under *Sphaerostephanos* by Holttum, justifies its inclusion in this genus. The pattern of the sporoderm in this genus is, however, not consistent.

Pronephrium and *Pneumatopteris*, similar to *Sphaerostephanos*, have very variable sporoderm, but the features of the gametophytic generation of these genera are very characteristic. In *Pronephrium* the mature prothallus is large, symmetrical, reniform, and bears small or large typical acicular hairs with numerous minute chloroplasts. Collenchyma-like deposition of wall material is another distinctive feature of the taxon.

The prothalli of *Pneumatopteris* are small but have a deep and broad apical notch slightly covered by upwardly projected overlapping wings. In this genus the midrib is composed of large and small hexagonal cells.

Large prothalli of *Ampelopteris* are characterised by unicellular glandular hairs with extracellular caps, a few small hyaline acicular hairs appearing at a very late stage of development, and peg-like outgrowths of very various shapes on the cellwalls. The sporoderm is also very distinct, its folded perine being closely beset with spines, spinules, and baculae.

Prothalli of *Thelypteris* are strongly asymmetrical, reniform, and have deep sinuses. Acicular hairs are few, but always long and hyaline. Collenchyma-like

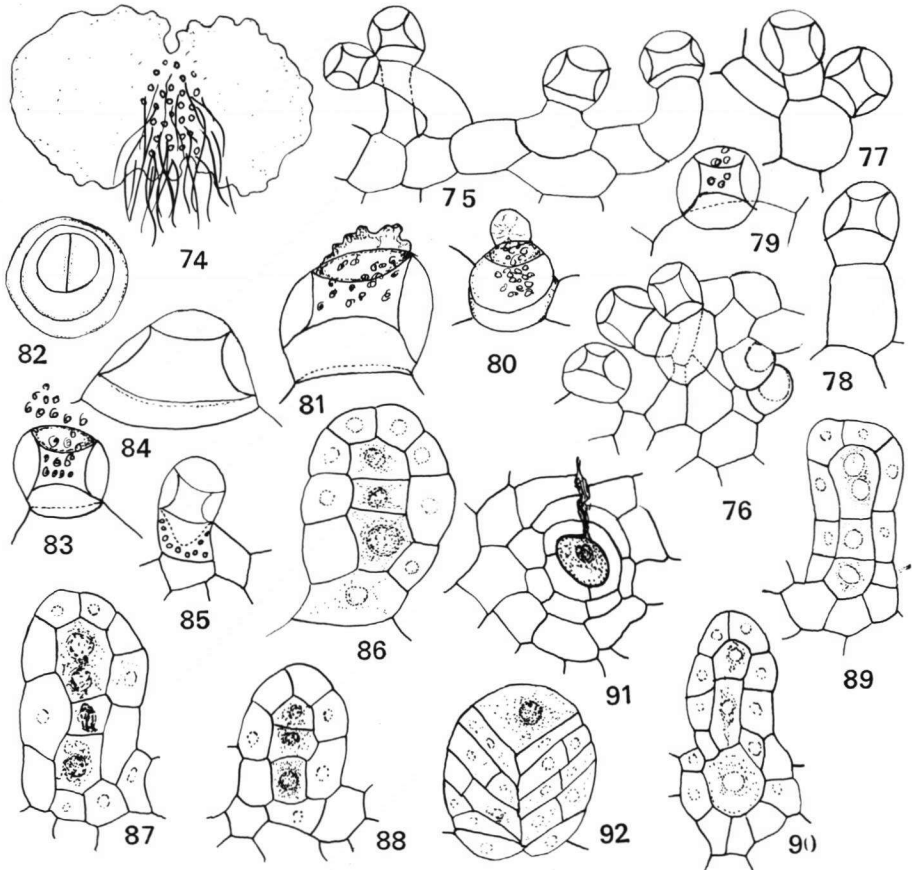


Plate IV. Figs 74–92. — Figs. 74 and 78, *Metathelypteris flaccida*. Figs. 75 and 88, *Pneumatopteris ecallosa*. Figs. 76 and 85, *Sphaerostephanos invisus*. Fig. 77, *Metathelypteris dayi*. Figs. 79 and 89, *Thelypteris palustris*. Fig. 80, *Cyclosorus gongyloides*. Figs. 81 and 82, *Christella dentata*. Figs. 83 and 90, *Pneumatopteris glabra*. Fig. 84, *Coryphopteris gymnopoda*. Figs. 86 and 91, *Sphaerostephanos penniger*. Fig. 87, *Coryphopteris arthrotricha*. Fig. 92, *Pronephrum nudatum*. 74, distribution of antheridia at the midrib of the thallus. 75, antheridia in a row. 76–77, antheridia in groups. 78, stalked antheridium. 79–81, globose and sessile antheridia. 82, divided cap cell. 83, antheridium with its pore. 84–85, different types of basal cell. 86–90, archaegonia. 91, nutritive layer around the zygote. 92, apogamous embryo. 74, $\times 7$; 75–78, 82, 85, $\times 150$; 79–81, 83, 84, 86–91, $\times 300$; 92, $\times 435$.

thickenings are lacking on the cellwalls of the wings. The sporoderm of the genus is covered with inconspicuous perispore.

Atkinson (1975b) similarly noted the diversity among the gametophytes of the Old World thelypteroids, *Mesophlebion crassifolia* (Bl.) Holttum, *Plesioneuron marattioides* (Alston) Holttum, and *Amphineuron opulentum* (Kaulf.) Holttum, and pointed out that the ornamentation of spores, the germination pattern, number of types of hairs present, the colour of glandular secretion of hairs, and other small differences support their separation into distinct groups. In the same year she (Atkinson, 1975a) found that the gametophyte of *Chingia pseudoferox* Holttum,

while conforming to the general thelypteroid pattern, deviates from it by the frequent presence on margin and surface of a multicellular structure, tentatively interpreted as a hair, characterised by a reddish brown terminal cell and simple glandular hairs borne laterally. This structure, according to her, sets apart the thallus of *C. pseudoferox* from other known thelypteroid gametophytes and supports the views of those taxonomists who propose generic segregation.

This study thus leads us to the belief that, similar to the features of the sporophytic generation, the characteristics of the gametophytes, if properly assessed, can conveniently be used in delimiting a taxon. The great diversity in the organization of the gametophytic generation of the thelypteroid taxa further leads to the conclusion that these plants must not be placed in a single genus as has been done by Morton (1963) and also later by Reed (1968). Though we are still ignorant about the gametophytes of a very large number of thelypteroid ferns, yet the information so far obtained probably indicate that the genera *Sphaerostephanos*, *Coryphopteris*, *Cyclosorus*, *Christella*, *Metathelypteris*, *Ampelopteris*, *Pneumatopteris*, *Pronephrum*, and *Thelypteris*, which have been circumscribed and recognised by Holtum (1971) on the basis of the sporophytic characters, are natural since they can also be delimited on the basis of gametophytic features.

The following is the tentative circumscription of the above taxa on the basis of the gametophytic generation:

Sphaerostephanos baramensis, *S. confertus*, *S. invisus*, and *S. penniger*:

Thallus large, cordate with long downwardly tapered base. Midrib long, narrow, strong, composed of uniformly large hexagonal cells. Multicellular hairs variable, simple, and glandular. Thickening on the walls of prothallial cells absent.

Coryphopteris arthrotricha and *C. gymnopoda*:

Thallus typically cordate with long, narrow, but strong midrib consisting of hexagonal cells delimited by a layer of narrow elongated cells on either side. Long unicellular flexuous hairs abundant; large glandular hairs without extracellular cap few and restricted to the midrib. Glandular hairs conspicuously yellow at maturity. Germ filaments terminated by papillate hairs. Thickening on the walls of the prothallial cells absent.

Cyclosorus gongyloides:

Old thalli large, reniform, but young ones typically cordate. Long flexuous hairs and glandular hairs with extracellular cap abundant. Walls of the prothallial cells with collenchyma-like deposition. Midrib broad, stout, consisting of uniformly large hexagonal cells. Germ filaments often terminated by papillate hairs.

Christella dentata and *C. parasitica*:

Old thalli irregularly circular and large. Apical cell stage in young prothalli lacking. Young prothalli broad with typical flat bases. Acicular hairs short and of two types: uniformly hyaline and with reddish brown tips. Multicellular glandular hairs quite frequent. Peg-like thickenings on the walls of the prothallial cells scattered. Midrib composed of similar cells never extended beyond the apical notch.

Metathelypteris flaccida and *Metathelypteris dayi*:

Prothalli large, irregularly circular, appreciably asymmetrical in old age. Reddish brown still acicular hairs and multicellular glandular hairs abundant. Very strong midrib consisting of a zone of hexagonal cells delimited on either side by a layer of narrowly elongated cells often extended beyond the apical notch.

Ampelopteris prolifera:

Old prothalli large and irregularly circular. Young ones typically cordate. Glandular hairs unicellular and always with extracellular caps. Acicular hairs variable, chlorophyllous and hyaline. Midrib strong, composed of uniformly large hexagonal cells. Peg-like thickenings simple, curved, and variously branched. Long flexuous hairs and reddish brown tipped acicular hairs conspicuously absent.

Pneumatopteris ecallosa and *P. glabra*:

Prothalli small with a flat or little abruptly tailed base, and a broad and deep apical notch lined on either side by upwardly projected overlapping wings. Midrib consisting of large and small hexagonal cells less developed and never extended upto the apical notch. Large glandular hairs without extracellular caps quite frequent close to the midrib. Apical cell of the prothalli quickly replaced by meristematic tissue.

Pronephrium nudatum:

Old thalli large and reniform but asymmetrical. Young ones typically roundish. Midrib composed of uniform hexagonal cells well developed. Chloroplasts in chlorophyllous hairs distinctively minute. Collenchyma-like thickenings sporadic but consistent in occurrence. Prothallial wings projected but never overlapping.

Thelypteris palustris:

Old thalli small, reniform, and conspicuously asymmetrical. Prothallial wings upwardly projected and overlapping. Young thalli reniform and with deep sinuses. Midrib spindle shaped, short, and composed of uniform hexagonal cells. Acicular hairs thin-walled, long and elongate. Collenchyma-like thickenings conspicuously absent.

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