STUDIES IN THE FAMILY THELYPTERIDACEAE II. A COMPARATIVE STUDY OF THE TYPE-SPECIES OF THELYPTERIS SCHMIDEL, CYCLOSORUS LINK, AND AMPELOPTERIS KUNZE

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INTRODUCTION (R. E. H.)

In the first paper of this series (Holttum, 1969) I gave a brief summary of taxonomic treatment of the family *Thelypteridaceae* in the present century, and stated that in my judgement no satisfactory subdivision of the family, as represented in the tropics of the Old World, had yet been achieved, the arrangements of Ching (1963) and Iwatsuki (1964) being in part inadequate because the authors were not sufficiently acquainted with the majority of species in the Malayan region and in the Pacific, which far outnumber those of mainland Asia.

I have been attempting a complete survey of all species of Asia, Malesia, and the Pacific, and it has become evident to me that a study of a wider range of characters than those used in most taxonomic species-descriptions is necessary in order to distinguish individual species clearly, and in order to provide data on which the delimitation of natural species-groups can be based. Therefore an essential preliminary is a detailed study of the morphology of the type-species of genera already proposed, as these species control the application of generic names. Such a study should indicate the nature of the differences between the species which by accident have become the types of genera, and will also provide standards against which the distinctive character-combinations found in newly recognized species-groups may be judged. The most- important generic names for the Old World tropics are *Thelypteris*, *Cyclosorus*, and *Ampelopteris*; in connection with the last-named, its resemblance to tropical American species included in *Goniopteris* Pr. (as re-defined by Christensen) necessitates a detailed examination also of at least one species of that genus.

There are some authors today who adopt the name *Thelypteris* for all species in the whole family. For those (such as myself) who regard the family as too diverse for convenient treatment in this way, it becomes important to know which tropical species, if any, are most closely associated with the type-species of *Thelypteris*, which has a north temperate distribution. The status of the generic name *Cyclosorus* is almost equally important, as a majority of Old World tropical Thelypteroid species have been ascribed to that genus, though Christensen's re-definition of it, based on New World species, is inconsistent with the current circumscription of the genus in the Old World by Ching and Copeland, a circumscription which I also adopted (with reservations) in my book on the ferns of the Malay Peninsula (1954).

The following statement by Sen and Mittra gives a detailed comparative account of the anatomy and morphology of the type-species of *Thelypteris*, *Cyclosorus*, and *Ampelopteris*, also of *Goniopteris obliterata* (Sw.) Pr., which is a near ally of the type species of *Goniopteris*, *G. vivipara* (Raddi) Brack.

Note on Nomenclature. Schelpe (1963) has shown that the earliest name for the species commonly known in recent years as *Cyclosorus gongylodes* is *Polypodium tottum* Thunb., published in 1800 and based on a South African specimen (Prodr. Fl. Cap. 172); Thunberg's epithet is now transferred to the genus *Thelypteris* as *T. tottum* (Thunb.) Schelpe. Morton (1967, pp. 73, 74) has listed other early names for the species. I do not wish here to make a transfer of Thunberg's epithet to *Cyclosorus*, as I am not ready to define that genus; and as Link specified Schkuhr's species *Aspidium gongylodes* (type from Guiana) as sole original species of his genus *Cyclosorus*, I prefer to use the name *C. gongylodes* for the type species of the genus in the present discussion. The Indian form of the species here described by Sen and Mittra is certainly closely similar to the form found in Guiana.

Similarly, Morton (1967, p. 71) has pointed out that there are earlier specific epithets for the species commonly known as *Thelypteris palustris* Schott, if this is taken in a broad sense (see Fernald, 1929), and I do not wish here to discuss the particular applications of these epithets. The name *T. palustris* is used to indicate the European form of the species, on which Schmidel based the generic name *Thelypteris*.

DESCRIPTIONS OF THE SPECIES (U. S. & D. M.)

Materials and Methods

Ampelopteris prolifera was collected from the Kalyani University campus. *Cyclosorus gongylodes* was collected from Sonapur (West Bengal). *Thelypteris palustris* was obtained from plants cultivated by R. E. Holttum in his garden at Kew, and from specimens collected by him in Holland. *Goniopteris obliterata* was from plants cultivated in the Royal Botanic Gardens, Kew, and we express our thanks for this material. Fixation was done in FAA, and the customary method of paraffin sectioning was followed. Sections were stained with safranin and Orange G. For gametophytic studies spores were sown in distilled water and on Beneck's solution with 2 % agar in glass containers. The assistance of Mrs T. Sen in drawing the figures is sincerely appreciated.

Ampelopteris prolifera (Retz.) Copel.

Chandra and Nayar (1968) have already published a detailed description of this species. Our examination was undertaken independently and completed before their publication appeared. We believe that their interpretation of the endodermis is inaccurate, and we have failed to find acicular hairs on the gametophyte. Though some of it duplicates the statement by Chandra and Nayar, we present our account here for conveinence of comparison with the other species.

A. prolifera is widely distributed in the Palaeotropics, from Africa in the west through South Asia to Australia and Polynesia. The plant usually grows near water or in wet ground. It produces extensive colonies both in exposed and in shady places mainly by its large proliferous fronds of indefinite growth. The axillary plantules, produced on fronds embracing trunks of trees in thickets, often clasp the bark of the trees with their roots and later, after the death of the parent frond, become epiphytic in habit.

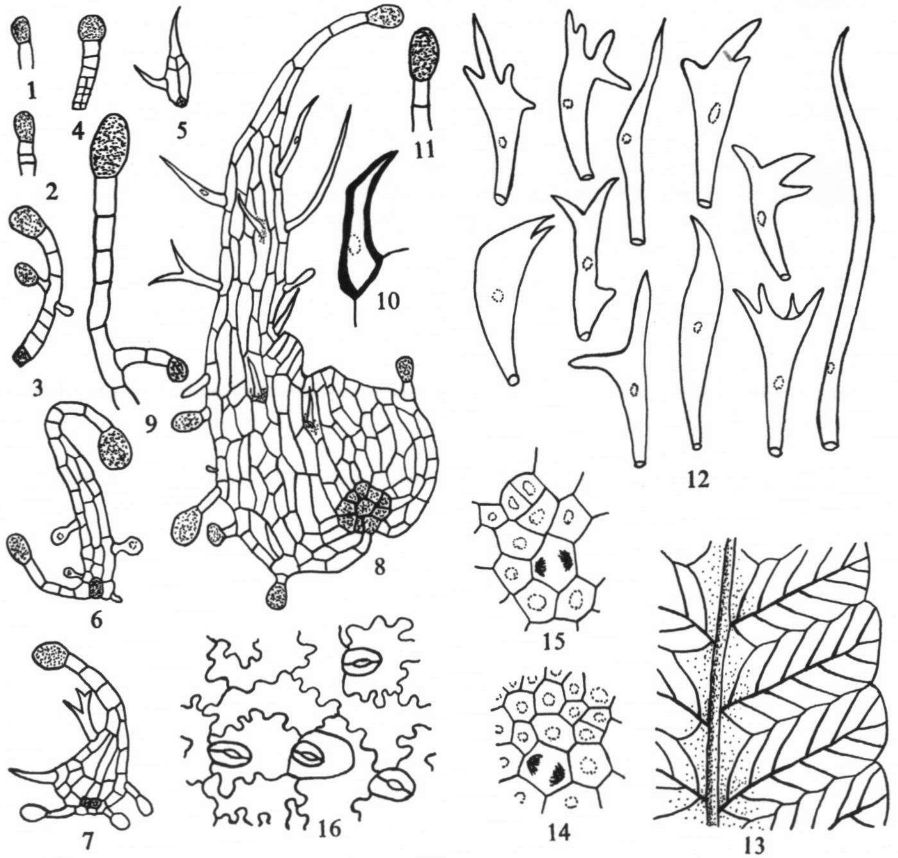
The rhizome is creeping, about 1 cm in diameter; it bears tufts of black branched roots with copious root-hairs. The older regions of the rhizome are almost naked; younger parts are densely covered with dark brown scales which are ovate with tapering apex.

Scale development begins with enlargement of a superficial cell, two or more cells removed from the apical cell of the rhizome. This initial cell soon divides into basal and outer cells (fig. 1). The basal cell remains undivided for a considerable period and later contributes to the formation of the stalk of the scale. Successive transverse divisions in the outer cell result in a short uniseriate hair-like filament, 7—12 cells long (fig. 2, 3). The terminal cell of the filament acquires dense hyaline contents and becomes club-shaped even when the filament consists of only three cells. Occasionally, however, the terminal cell may develop into a sharp-pointed hair with thickened walls (fig. 5). Longitudinal divisions of the cells near the basal region of the filament initiate flattening of the scale (fig. 4). Marginal hairs begin to develop on scales even when they are uniseriate; the hairs may be glandular or pointed. Glandular hairs may be unicellular or multicellular, branched (fig. 6, 7, 9) or unbranched, while the pointed hairs are always unicellular. Pointed hairs may be unbranched or forked but are never cruciately branched. Numerous superficial hairs, resembling marginal unbranched pointed hairs, also develop (fig. 8). During the later stages of development of the scale the stalk cell by repeated divisions becomes multicellular and some of the cells, at the junction of stalk and body of the scale, bulge outwards and expand basally to form a hood-like structure, making the scale appear peltate (Chandra and Nayar figure a larger scale, lacking superficial hairs, with broadly cordate base).

A single relatively large initial cell occupies the apex of each rhizome-branch; it protrudes slightly from the surface of the promeristem and is overarched by numerous scales at various stages of development. It is tetrahedral, conspicuously vacuolated, and cuts off segments at its three faces. Two or three millimetres behind the apex, cell elongation and tissue differentiation into protoderm, procambium, and ground meristem take place. Rhizomes of very young plants have a protostelic vascular cylinder; this is replaced by an amphiphloic siphonostele after the rhizome has produced two or three leaves, and with further development there is change to a dictyostelic condition. The meristeles are generally hadrocentric but may be bicollateral. The xylem consists of tracheids and small thin-walled parenchymatous cells (fig. 17). Tracheids of the protoxylem possess a delicate unlignified primary wall with a series of annular thickenings inside it; sometimes the distantly placed rings are interconnected by a vertically or obliquely oriented helical band (fig. 32). Protoxylem elements may also possess single or double helical bands or a single annular-helical band (fig. 31, 33). Tracheids of the metaxylem are scalariform and have trans-edge opposite as well as alternate pittings, the pits elongate or oval (fig. 35, 36). In a concentric meristele, the phloem layer is usually 4—6 cells in thickness, but in a bicollateral one the phloem in places may consist of a single layer of cells. The pericycle is parenchymatous and of variable thickness.

Cortex and stele are separated by a well-defined endodermis; its cells have Casparian strips only on their radial walls. The hypodermal region of the cortex is parenchymatous, thin-walled, but later may become thick-walled; below the hypodermal region are dark brown sclerified cells, while the inner part of the cortex is almost hyaline, the cells full of starch. The cells surrounding the endodermis, however, lack starch grains and have considerable thickenings on both radial and outer tangential walls (fig. 17); Chandra and Nayar (1968) interpreted this layer of ground tissue as endodermis. The pith is parenchymatous and its cells are densely filled with starch. Scattered within the parenchymatous cells of the inner cortex and pith are a few isolated or small groups of 2 to 4 thick-walled, slightly elongated, light to dark brown cells; when old, such cells have ramified pits in their walls.

The leaf-gaps are 10—11 mm long and 3—4 mm wide, fusiform in shape, spirally



Ampelopteris prolifera. Figs. 1—8. Scales in the stages of development, × 50; 9. Glandular branched hair borne on the margin of the scale, × 130; 10—12. Different types of foliar hairs, × 130; 13. Part of a lamina showing pattern of venation, × 7; 14 and 15. Stomata in the stages of development, × 300; 16. Mature stomata, × 140.

arranged, and dissect the vascular cylinder into a compact reticulum (Chandra and Nayar report obovate leaf-gaps). A pair of leaf-traces depart from a gap at a point half-way from its base to its apex. Leaf-traces originating from margins of gaps on the dorsal side of the creeping rhizome pass directly through the cortex, but those from lateral or ventral gaps have a short to relatively long curvature through the cortex and the petioles they enter are displaced laterally. Thus fronds appear to be borne only dorsally and laterally.

The fronds are simply pinnate. Sterile fronds have flagelliform tips and appear to be of indefinite growth. Fertile fronds develop a terminal pinna; they may be 120 cm or more long. Throughout the petiole and rachis on the adaxial side is a groove; costae of pinnae are similarly grooved, but the grooves of rachis and costa are not confluent (fig. 18, 21). On the young petiole and rachis are numerous hairs which are unicellular, or multicellular with glandular tip (fig. 11, 12); the unicellular hairs may be simple or variously branched. Simple acicular hairs are borne on the upper surface of costae; the lower surface in large fronds bears only scattered small, thin, broad scales, though on sterile fronds from developing rachis-buds there may be many acicular hairs on the lower surface of costae. At the base of each pinna, on the abaxial side, is a patch of aerating tissue which is dark green and slightly swollen; it does not develop into an elongate aerophore. Pinnae are commonly 5—22 × 1—2 cm; their edges are crenately lobed, and there is at most only a short sinus-membrane connecting the lobes. The veins anastomose in the manner usual in this family (fig. 13); excurrent veins are rarely free, and only a few veins in each lobe run to the cartilaginous margin. The vein-endings contain tracheids only; these are few, short, and have a comparatively wide lumen with annular helical thickenings. The cells in contact with the terminal tracheids are not different from other mesophyll cells; thus there is no epithem layer. Further, there are no suberized cells adjacent to the terminal tracheids, and the upper epidermis overlying the tracheal ends does not develop any stoma or pore. The lamina is thin; on its margin are many short-pointed, straight or curved, thick-walled unicellular hairs (fig. 10).

The epidermis and sclerotic hypodermal layer of both the petiole and rachis are interrupted laterally by aerating tissue on either side. The two petiolar bundles are embedded in thin-walled tissue. They are hadrocentric, and in transverse section the xylem mass appears as an E or inverted E; each xylem strand has two protoxylem groups in its inner face (fig. 18). The phloem surrounds the xylem, or it becomes interrupted at the two opposite poles of the xylem plate (fig. 19). The petiolar bundles have a thin-walled endodermis and pericycle of 1—3 layers. Surrounding the endodermis there is a sheath of asymmetrically thickened cells with pits on their thickened walls.

The mesophyll of the leaf-lamina is undifferentiated; it consists of 3—4 layers of conspicuously armed, chlorophyllous, thin-walled cells with intercellular spaces. Cells of both upper and lower epidermis have thickened peripheral walls and sinuous lateral walls (fig. 21). Stomata are only on the lower epidermis; ontogenetically they are of syndetocheilic type (fig. 14, 15). Each stoma is associated with one or two subsidiary cells (fig. 16). The walls of the guard cells are unevenly thickened and there are ledges of cutinized material projecting over the external opening of the stomatal pore.

Sori are elongate on the distal parts of veins. The receptacles are raised and have sporangia af different stages of growth, protected by unbranched multicellular paraphyses, each ending in a smooth club-shaped cell with orange coloured contents (fig. 22). A sporangium-stalk is 3—4 cells long and 2 cells thick except towards the apex where it is 3-celled. The vertical annulus consists of 15—19 cells, the epistomium of 2—4, and hypostomium of 3 or 4 cells. The sporangial stalk bears one or more trichomes on the outer side of the second, third, or fourth cell from the top. These trichomes are similar to the paraphyses. No pointed cells are developed on the sporangium stalk, nor any hairs near the annulus (though Chandra and Nayar report the rare presence of a sessile glandular hair on a cell of the annulus).

The receptacle makes its appearance on the lower surface of the lamina at some distance from the margin; as a multicellular upgrowth of rounded form. The cells of this upgrowth can be traced to the submarginal meristem of the developing lamina. Certain superficial cells of the receptacle begin to grow out as paraphyses, while others soon become recognizable as sporangial initials. A sporangial initial enlarges and divides transversely into an apical and a basal cell (fig. 23). The apical cell increases in size and by two lateral oblique walls and an upper periclinal wall differentiates a primary sporogenous cell surrounded by 3 peripheral cells (fig. 24—27). The former gives rise to a 2-layered tapetum and 16 spore-mother-cells (fig. 29, 30). The peripheral initials divide to form a sporangial wall one cell thick (fig. 28—30). In the meantime the basal cell produces two primary rows of stalk cells; a third row of stalk cells later develops as a downward projection of the basal cell of the hypostomium. A sporangium produces 64 spores. They are bilateral, monolete, plano-convex in lateral view, ovate in polar view, and have a thick smooth exine surrounded by a folded and densely spinulose perine.

The roots are slender and branched; they develop from any part of the rhizome and do not show any relationship with the development of leaves. A transverse section of a root shows the single-layered epidermis with many unicellular hairs, followed by a parenchymatous cortex packed with starch grains, a single-layered endodermis, pericycle 2 cells thick, and a diarch xylem plate with laterally placed phloem. In the older parts of the root the cortex becomes sclerotic (fig. 20).

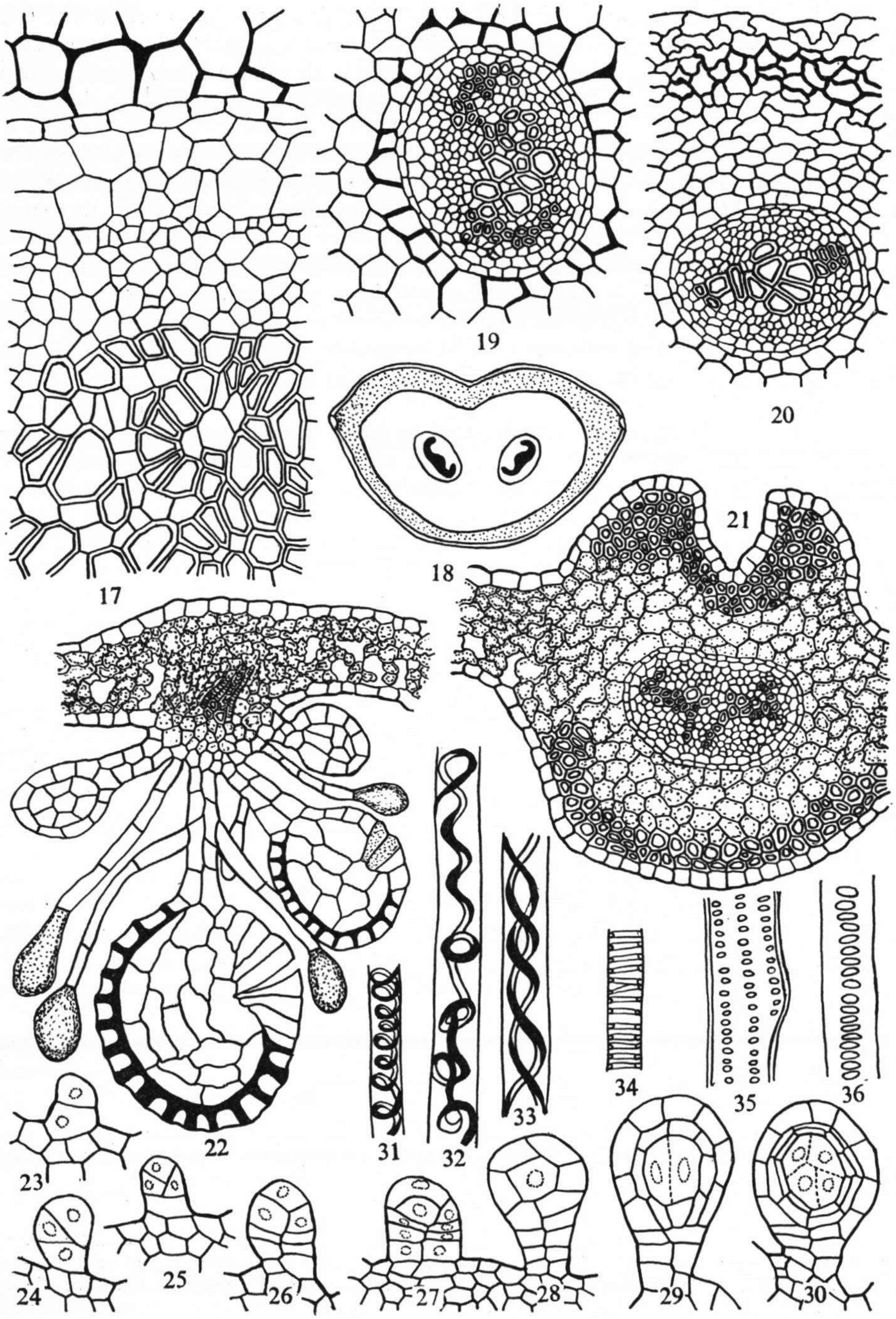
The gametophyte arises as a short filament followed by a spatula which becomes cordate at maturity. In over-crowded culture the young prothallus is a variously branched filament. The apical meristematic cell of the prothallus is always formed from the terminal cell of the germ filament. Mature gametophytes develop filamentous or cordate branches. Hairs with extra-cellular apical cap-like secretions originate both at the margin and on surfaces of the prothallus. In old prothalli peg-like outgrowths develop on the surfaces of the wings. Chandra and Nayar (1969) have reported the formation of unicellular, elongated, non-chlorophyllous, acicular hairs on the prothallus of this species, but we have not seen them. The antheridia and archegonia are of the usual type found in higher ferns.

Cyclosorus gongylodes (Schkuhr) Link

This species has a pantropic distribution; it is well represented in India where it grows in open swampy places and by the sides of ponds.

The slender creeping rhizome is superficial or shallowly buried in surface litter or rarely in soil, and has scattered tufts of roots. Plants growing near ponds often spread their branches in water, where they become entangled. Rhizome-branches are dichotomous or due to differential growth become monopodial; occasionally the tips of branches curve upwards and become suberect. Younger parts are densely covered with non-peltate scales. At its apex a scale bears a swollen, thin-walled, glandular cell. Similar glandular cells, borne on slender, unicellular or multicellular, branched stalks, are borne on some of the marginal cells of the scale (fig. 41). Unicellular, stiff, pointed hairs are also borne by marginal cells (fig. 40). Two-celled glandular hairs and unicellular pointed hairs are developed on both surfaces of the scale (fig. 42, 43). The scales originate as uniseriate hairlike appendages (fig. 37, 38) and their mode of development is almost similar to that of scales of *Ampelopteris prolifera*, the only difference being that at no stage during development do the scales appear peltate (fig. 39—41). Mature scales are light brown in colour, and cells occupying the central region have peg-like thickenings of various forms on their walls. The rhizome is fleshy with thin-walled epidermis and

Ampelopteris prolifera. Figs. 17. Transverse section (T.S., of a part of meristele of rhizome, × 150; 18. T.S. of a petiole, × 7; 19. T.S. of a petiolar bundle, × 90; 20. T.S. of a root, × 90; 21. Vertical section (V.S.) of a pinna passing through the midrib, × 90; 22. V.S. through a sorus, × 150; 23—30. Sporangia in the stages of development, × 300; 31—36. Tracheids from the rhizome, × 400.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a hypodermal sheath of comparatively thin-walled sclerenchyma 4—6 cells thick. The cells of the ground tissue are parenchymatous and full of starch grains. The most distinctive feature of these cells is the deposition of additional wall material only on the radial walls. The vascular cylinder of the rhizome is a dictyostele. It is pierced by closely or distantly placed, spirally arranged, elongate fusiform leaf-gaps. The cells immediately outside the endodermis, unlike those of *Ampelopteris*, do not show any special type of thickening on their walls. The endodermal cells have thickening only on their radial walls (fig. 50). The pericycle consists of 1 or 2 rows of thin-walled cells. The thin layer of phloem consists of elongate sieve cells and a few of parenchyma; it surrounds the xylem or is restricted to either side of the xylem plate. The xylem is mesarch and consists of tracheids with double helical bands, and with annular helical hybrid type of thickening in the protoxylem. Metaxylem elements are scalariform and have elongated oval pits (fig. 56—58). Thin walled parenchyma cells, isolated or in groups, occur between the tracheids (fig. 50); they are comparatively short cells and often contain tanniferous substances.

The fronds are borne spirally, well spaced on the rhizome; they are bipinnatifid, the basal pinnae hardly shortened. Petiole (fig. 47), rachis, and costae are grooved on the adaxial surface as in *Ampelopteris*. On the lateral surfaces of the rachis and petiole there is a continuous line of aerating tissue; the patch of aerating tissue at the base of each pinna is very small. Scales like those of the rhizome protect the young fronds; many of them are caducous at maturity but some always persist on lower surfaces of costae. Unicellular pointed hairs and multicellular glandular hairs are variously distributed on the frond (fig. 44, 45). Acicular hairs are always present on the upper surface of costae. A remarkable feature is the presence of numerous sessile, bright orange glands on the under-surface of lamina and veins. The pinnae are not deeply lobed and have oblong subdeltoid segments with acute apices. There are 5—10 pairs of veins in each segment; the lowest veins from adjacent costules meet and unite to form an excurrent vein which runs to the bottom of the sinus-membrane which joins the bases of two lobes. The next acroscopic vein frequently unites with the excurrent vein, while the corresponding second basiscopic vein usually joins with the membrane near the sinus; remaining veins run to the margin (fig. 46).

Fig. 47 represents a transverse section of the petiole, which in structure is similar to that of *Ampelopteris*. The important differences are that some of the cells of the ground tissue have thickening only on their radial walls and that their intercellular spaces are more or less angular. Further, the cells just outside the endodermis do not show any additional thickening on their walls (fig. 48). The epidermal cells of the lamina are chlorophyllous and have a sinuous contour. Stomata on the abaxial epidermis are profuse; each of them is almost encircled by a subsidiary cell. Ontogenetically the stomata are of syndetocheilic type. Mesophyll cells are more or less oval or angular in outline and have short arms (fig. 49). The few rows of cells which form the sinus-membrane lack chloroplasts and on drying form a prominent ridge on the abaxial side.

Fertile fronds are similar to sterile ones. Sporangia are borne on round raised receptacles

Cyclosorus gongylodes. Figs. 37—41. Scales in the stages of development, × 90; 42 and 43. Superficial hairs of a scale, × 130; 44 and 45. Foliar hairs, × 90; 46. Part of a lamina showing pattern of venation, × 7; 47. T.S. of petiole, × 7; 48. T.S. of a petiolar bundle, × 90; 49. V.S. of a pinna passing through the midrib, × 90; 50. T.S. of a part of meristele of rhizome, × 150; 51. V.S. of sorus, × 140; 52. Mature sporangium, × 140; 53. An indusium, × 50; 54. A spore, × 450; 55. A magnified part of the spore wall, × 1000; 56—58. Tracheids from the rhizome, × 300.


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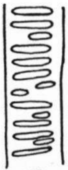
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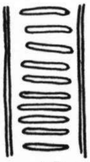
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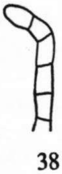
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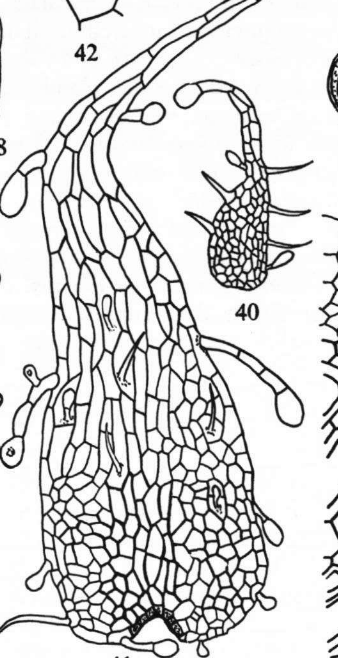
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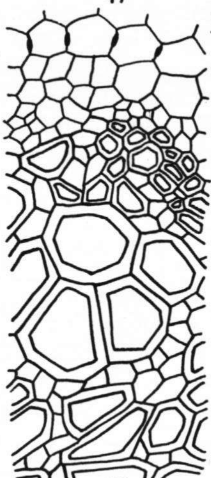
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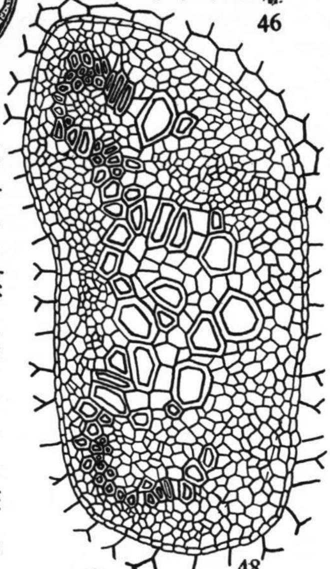
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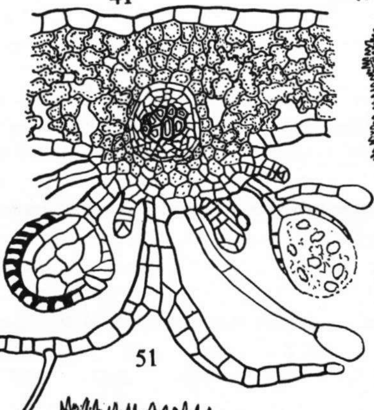
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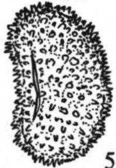
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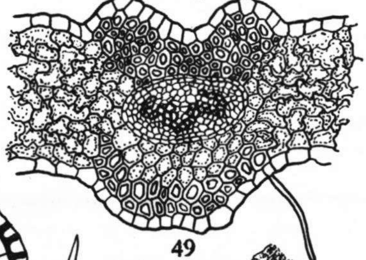
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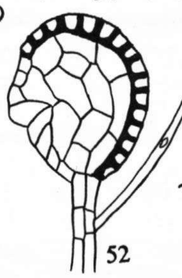
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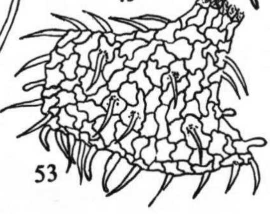
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(fig. 51) situated on the veins in a medial position; the lowest veins rarely bear receptacles. Each sorus is protected by a reniform indusium opening away from the costule. The indusium is one cell thick and develops profuse unicellular pointed and glandular hairs at its margin and also on its surface (fig. 53). A mature sporangium has a short stalk about 3 cells long (fig. 52). In a young sporangium the stalk is 2 cells in thickness, but towards maturity becomes 3 cells thick near the top due to downward protrusion of the basal cell of the capsule-wall on one side. One of the distal cells of the stalk either develops a long, pointed, unicellular seta (fig. 52) or a uniseriate multicellular hair with glandular tip (fig. 51). The annulus is vertical and consists of 14—18 cells; there are 2 or 3 cells in the epistomium, 3 or 4 in the hypostomium. Multicellular glandular paraphyses occur between the sporangia. The spores are bilateral, monolete, and possess densely spinulose and baculate exine. There appears to be no perine (fig. 54, 55). On an average the spores measure 28.5 μ × 45 μ × 32 μ (P × E × E1).

Roots develop on all sides of the rhizome. Many of them arise in pairs immediately after the opening of a leaf-gap from its two margins and immediately before the leaf-traces depart, while the remaining ones develop from any point on the outer margin of the meristeles. Internally they resemble roots of *Ampelopteris* in all essential details.

Gametophyte. Cracking of the spores took place 5—7 days after sowing in the culture solution. The percentage germination was rather low at first, but after a few weeks became comparatively high. There is a great enlargement of the primary cell before the first division occurs to cut off the primary rhizoid-bearing cell. A few chloroplasts appear and persist for a short time not only in the first rhizoid but also in a few subsequent ones. The prothallial cell by repeated transverse divisions forms a uniseriate filament 3—10 cells long; often such filaments produce uniseriate multicellular branches by lateral proliferation of any of their intercalary cells. Occasionally, however, the formation of filamentous forms is omitted and the developing prothallus becomes a small plate at a very early stage. The terminal cell of the 3—10-celled filament behaves in two ways: either (i) it divides by vertical walls ultimately to produce an apical meristematic cell, or (ii) it develops a papillate hair at its tip. In the latter case the subterminal cell undergoes oblique divisions and produces an apical meristematic cell. The remaining cells of the filament except the basal 1—2 cells, in both cases, undergo longitudinal divisions. In any case the apical meristematic cells are not very active until the prothallus becomes spatulate.

The mature prothallus is cordate with a more or less entire margin. It has a broad thick midrib and thin wings. The cells of the wings are thin-walled, but the cells in old prothalli as in *Ampelopteris* develop peg-like outgrowths of very various form on their walls. Numerous hairs are produced both on the margin and surfaces; the hairs are unicellular, thin-walled, sparsely chlorophyllous, club-shaped, and have cap-like waxy secretion at the tip. The rhizoids which develop profusely on the midrib and also elsewhere on the wings become brown with age; they have a swollen base and bulbous tip.

Nayar and Chandra (1963) report acicular hairs 1—3 cells long, with pointed dark brown apices on prothalli of *C. parasiticus* and *C. aridus*; Kachroo found the same on prothalli of *C. molliusculus*. No such hairs were found by us on *C. gongylodes*. For a note on the significance of this, see Holttum's comments in the concluding section of this paper.

In cordate thalli of *C. gongylodes* sex organs develop on the midrib and also on adjoining areas of the wings. Structurally and ontogenetically both antheridia and archegonia are very similar to those of *Ampelopteris*. A very striking feature of the old gametophyte of *C. gongylodes* is that some superficial wing cells proliferate and produce an elongated, vertically orientated cell which later develops an antheridium at its tip.

Thelypteris palustris Schott

Like the tropical *Cyclosorus gongylodes*, this temperate-zone species grows in wet ground in rather open places. The long creeping rhizome is irregularly branched, black externally, and its younger parts are protected by scales. The scales are brown, non-peltate, and bear pointed and glandular hairs on margin and surfaces (fig. 62, 65, 67). The glandular hairs may be unicellular or consist of two cells (fig. 63, 66). Some of the marginal hairs may be branched with glands on each branch (fig. 66). The scales during their ontogeny pass through a uniseriate filamentous stage (fig. 59—61).

The vascular system of the adult rhizome is dictyostelic (fig. 76), being dissected by radially arranged fusiform leaf-gaps. The meristeles are mostly bicollateral, very rarely concentric. The tracheids of the protoxylem have annular and annular-helical thickenings; the helical band is single-stranded at one region but may become double-stranded at another by forking (fig. 83). Some of the tracheids are thin-walled and have poorly lignified closely packed rings which are interconnected by vertical, broad, wavy strands. A few annular rings in such cases may not touch the tangential wall of the tracheids. The early metaxylem elements may have simple reticulate thickening (fig. 85) while the late metaxylem ones are simple-pitted. The pits are narrow and may be elongated or oval in outline (fig. 84). The endodermal cells possess prominent Casparian strips (fig. 77) and have no tanniferous contents. The cells of the fundamental tissue are thin-walled parenchyma with profuse intercellular spaces and do not contain starch grains. Excepting the hypodermal sclerotic cells, no other cells in the ground tissue have any deposition of lignin on their walls.

The fronds are spirally arranged, 1—3 cm apart. At the very base of the petiole there is no furrow on the adaxial side (fig. 73) but a shallow flattened groove appears a little higher up. As in *Ampelopteris* and *Cyclosorus gongylodes*, the two leaf-traces, in cross section each resembling a hippocampus (fig. 74), enter the petiole. The characteristic feature of the petiole is that all the cells of the ground tissue except the hypodermal ones are thin-walled and have no deposition of additional material on their walls. The lamina is papyraceous and the veins are forked, free, reaching the very margins of lamina-lobes (fig. 70). At the ends of the veins are a few elongated tracheids closely grouped together; there are no hydathodes associated with them. The mesophyll cells are more or less oval and they have very few small arm-like projections (fig. 75). The stomata are of syndetocheilic type (fig. 72) and may have one or two subsidiary cells (fig. 71). Sharp pointed unicellular hairs and 2-celled glandular hairs are developed on the lamina and on the veins of young fronds (fig. 68, 69). Some thin scales, of various sizes, up to ½ mm or more long, are usually also persistent on the lower surfaces of costae of pinnae. The receptacles are round, raised, and situated on the acroscopic branch of each vein (fig. 78). The important features of the sporangium are the presence of 1- or 2-celled glandular hairs on the stalk and the development of unicellular baloon-like hairs on the sporangial jacket (fig. 79). There are 14—18 cells in the annulus; the epistomium consists of 3—4 cells, the hypostomium of 4. The reniform indusium is provided with glandular hairs both on margin and outer surface (fig. 80). Spores are bilateral and have spinulose, spinose, and baculate exine and apparently no perine (fig. 81, 82). A spore measures about 25.5 μ × 41.5 μ × 27 μ (P × E × E1).

The roots are similar to those of *Cyclosorus gongylodes* in structure and development.

A spore on germination produces a germ-filament composed of 5—8 short barrel-shaped cells. Soon a prothallial plate is formed and an apical meristematic cell is differentiated in the terminal cell of such a filament. Mature prothallia are small, cordate, and develop profuse papillate hairs on the margin and surface. The hairs are unicellular, thin-walled, elongate-papillate, and chlorophyllous; they secrete a waxy extracellular cap at the apex of each hair. No acicular hairs are produced and no small peg-like outgrowths from cells of old gametophytes.

Goniopteris obliterata (Sw.) Pr.

This species is native in Jamaica, Cuba, and Central America. The rhizome is short-creeping and may become ascending or erect. The scales are rigid, non-peltate (fig. 92), dark brown in colour. Stellate unicellular hairs of very various forms develop from almost all the marginal and superficial cells of the scale (fig. 92, 94). In addition to these hairs, a few unicellular glandular hairs may be borne on the marginal cells of the scale (fig. 93). The tips of the scales are always glandular (fig. 91). As in the other species described above, the scales of *G. obliterata* pass through a filamentous stage during their ontogeny (fig. 86—92).

The rhizome in transverse section is irregular in outline due to close attachment of leaf-bases (fig. 105). The vascular cylinder is dictyostelic and is dissected by numerous closely arranged leaf-gaps. All the meristeles are hadrocentric and have a comparatively thicker zone of phloem (fig. 106). The protoxylem consists of annular and annular-helical elements (fig. 109) while the tracheids of the metaxylem have elongated to oval pits (fig. 107, 108). The epidermis consists of cubical cells and bears variously branched stellate hairs in addition to the scales. The well-differentiated hypodermis is composed of sclerotic cells, several cells in thickness. The parenchymatous ground tissue contains almost uniformly thick-walled cells, compactly arranged. An important feature is that many cells of this region show crystalline inclusions. Outside the endodermis of each vascular strand there is no layer of cells with special type of thickening. No sclerotic patches or isolated sclerenchymatous cells have been found within the ground tissue (fig. 106).

The fronds are often proliferous and develop axillary buds. Numerous thin-walled, unicellular, stellate hairs of very various form (fig. 99), thick-walled, sharply-pointed, unicellular hairs (fig. 98) often forked at the tip (fig. 97), and multicellular glandular hairs with or without lateral glands or stellate hairs (i.e., compound hairs) are borne on the different parts of the frond (fig. 95, 96, 100—102). A cross section of the petiole at its base shows that the aerating tissues are situated on the lateral surfaces and there is a furrow on the adaxial surface (fig. 103). The patch of aerating tissue at the base of each pinna is small. Structurally, the petiolar bundle is more or less similar to those in the other species (fig. 104). Anastomosis of veins is often irregular and the ends of veins sometimes continue along the margin (fig. 110—113, 115); several pairs from adjacent costules unite, and a few remain free near the apices of pinna-lobes (fig. 114). Stomata are usually

Thelypteris palustris. Figs. 59—61. Scales in the stages of development, × 90; 62. Mature scale, × 40; 63. Tip of a scale, × 130; 64—67. Superficial and marginal hairs of a scale, × 130; 68 and 69. Foliar hairs, × 140; 70. Part of a lamina showing pattern of venation, × 7; 71 and 72. Stomata in the stages of development, × 140; 73. T.S. of petiole, × 7; 74. T.S. of petiolar bundle, × 140; 75. V.S. of lamina, × 300; 76. T.S. of rhizome, × 7; 77. T.S. of a part of meristele of a rhizome, × 140; 78. V.S. through a sorus, × 130; 79. Mature sporangium, × 130; 80. An indusium, × 50; 81. A spore, × 450; 82. A magnified part of the spore wall, × 2100; 83—85. Tracheids from rhizome, × 400.


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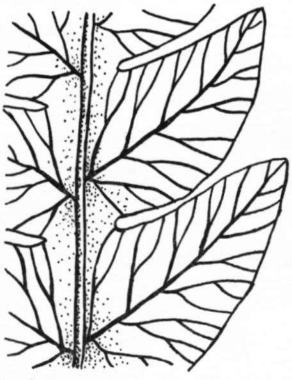
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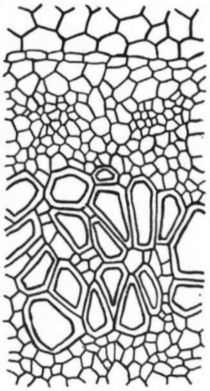
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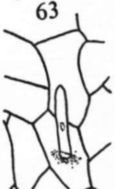
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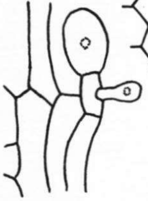
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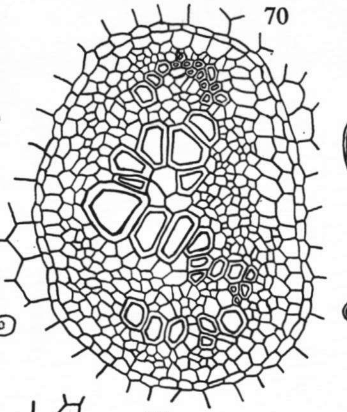
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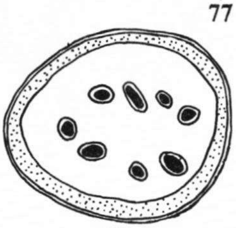
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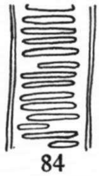
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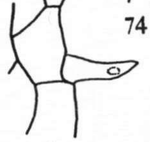
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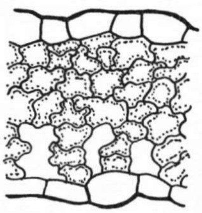
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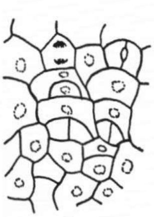
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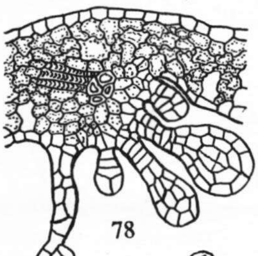
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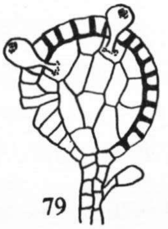
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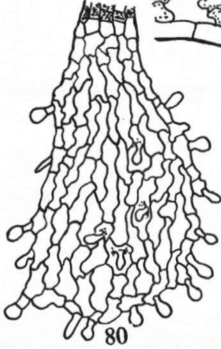
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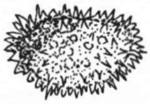
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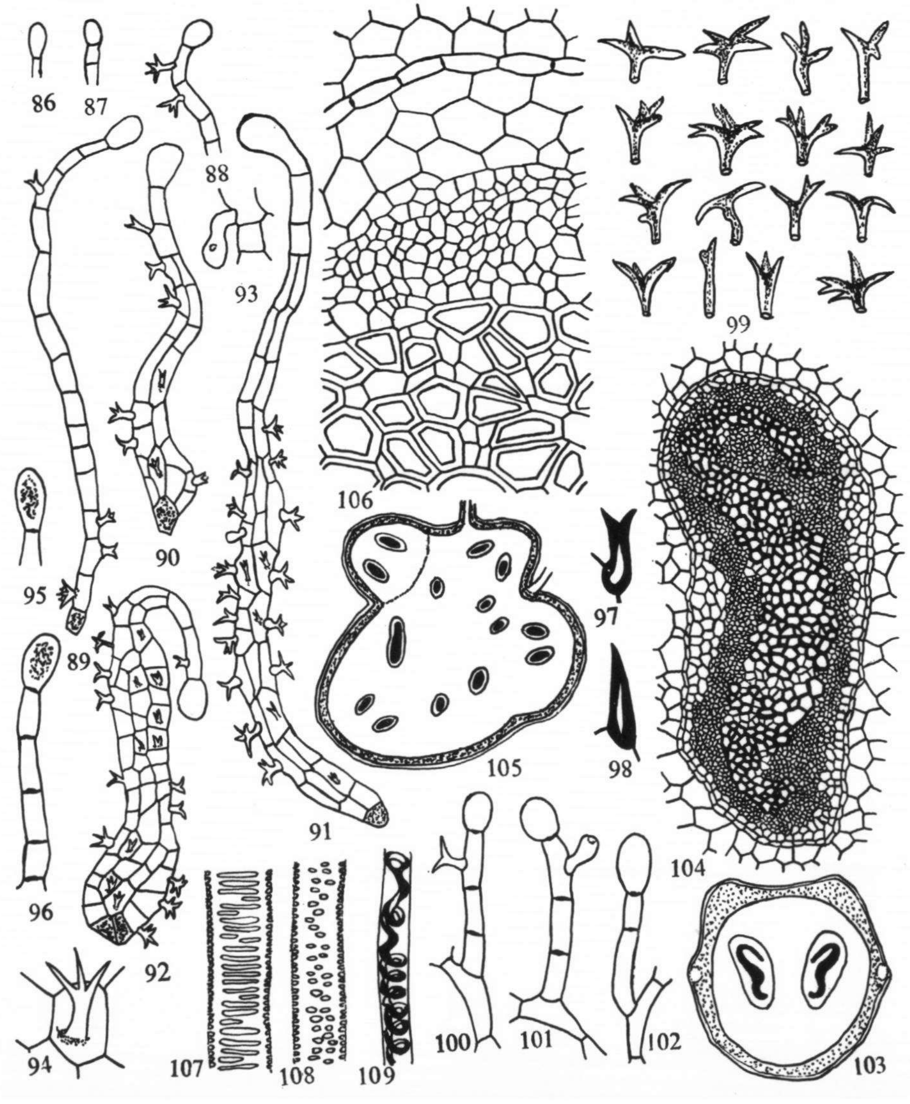
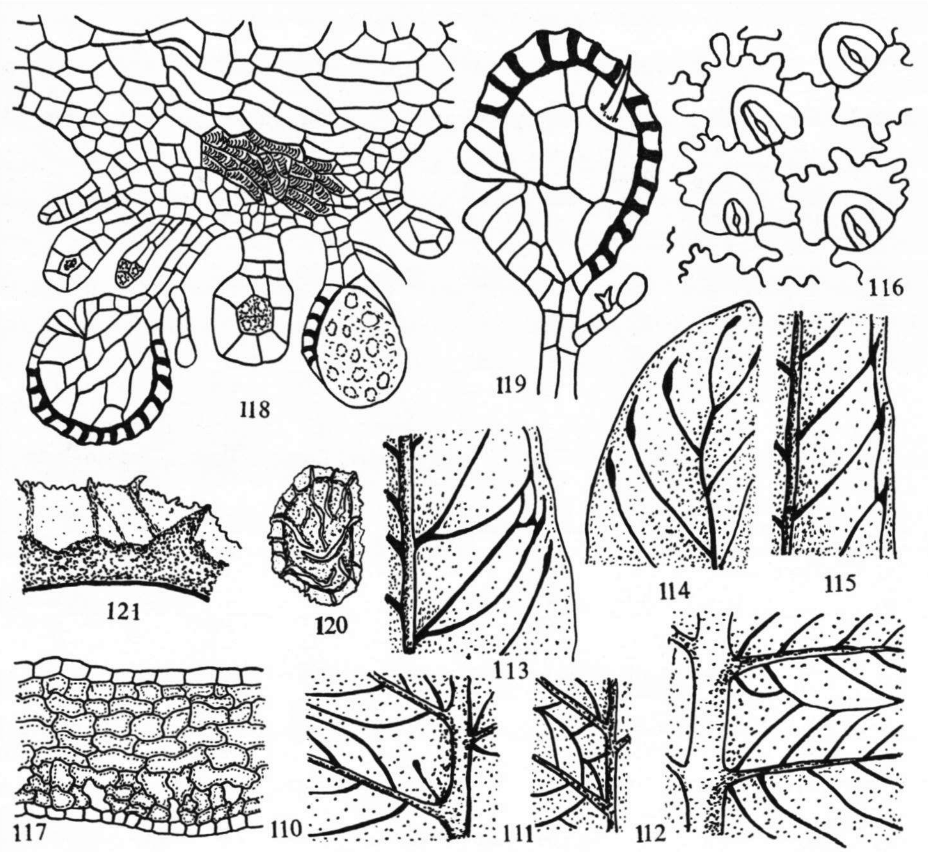


Goniopteris obliterata. Figs. 86—92. Scales in the stages of development, × 90; 93. A glandular hair on the scale, × 130; 94. A stellate hair, × 450; 95—102. Different types of foliar hairs, × 140; 103. T.S. of petiole, × 7; 104. T.S. of a petiolar bundle, × 50; 105. T.S. of rhizome, × 2; 106. T.S. of a part of meristele of rhizome, × 170; 107—109. Tracheids from rhizome, × 220.

associated with two subsidiary cells (fig. 116). The mesophyll cells are rather elongated and have a few short arms (fig. 117).

Soral receptacles are raised, round, and appear on the veinlets (fig. 118). Sporangia are oval to globose and have stalks 3—4 cells long (fig. 119). Unicellular pointed hairs and multicellular glandular hairs with unicellular stellate cells borne on them (i.e. com-



Goniopteris obliterata. Figs. 110—112. Pattern of venation near the costal region of the lamina, × 3.5; 113—115. Pattern of venation near the margin of the lamina, × 7; 116. Mature stomata, × 140; 117. V.S. of lamina, × 140; 118. V.S. of a sorus, × 170; 119. A mature sporangium, × 130; 120. A spore, × 300; 121. Part of a magnified spore wall, × 2100.

pound hairs) develop on the sporangial stalk (fig. 118, 119). Sharply pointed unicellular hairs originate on the sporangial jacket. The annulus is composed of 14 cells; the epistomium of 2, the hypostomium of 3—5 cells (fig. 119).

The spores are bilateral and monolete; they have a well-developed hyaline folded perine (fig. 120). Both the exine and the perine are spiny and tuberculated (fig. 121). A spore measures about 30 μ × 51 μ × 37 μ (P × E × E1).

Roots originate from all parts of the rhizome. At the base of each petiole, always a pair of roots originate from the margins of the confronting leaf-gap.

Nothing is known about the gametophyte of this species, but the reported formation of stellate hairs on the gametophytes of *Thelypteris* (sect. *Goniopteris*) *biollyi* (Christ in Pitt.) Proctor (Atkinson & Stokey, 1964) is certainly significant.

CONCLUSIONS AND DISCUSSION (R. E. H.)

Characters common to the four species

Frond-form: all species have simply pinnate fronds, the pinnae with edges parallel for most of their length and more or less deeply lobed; the lowest pinnae are not or little shorter than those next above them.

Upper surface of rachis and costae are grooved, but the costal groove is not confluent with the rachis-groove.

Aerophores. The small patch of aerating tissue at the base of a pinna does not form a prominent aerophore in any species.

Unicellular acicular hairs are always present on the upper surface of rachis and costae, and often elsewhere on surfaces of the frond or of its scales, indusia, or sporangia.

Position and general structure of sori are similar in all, except that there is no indusium in *Ampelopteris prolifera* and *Goniopteris obliterata*, and in the former that sporangia are distributed along the veins to some extent.

Vascular structure of rhizome and petiole, in almost all details, is similar in all.

Gametophytes of all are cordate when mature, and all bear unicellular hairs with wax-covered tips; antheridia and archegonia are all similar in structure and position.

Principal differences between the four species

Acicular or non-glandular unicellular hairs on scales, lamina-surface, stalk and body of sporangium. These are simple in *Thelypteris palustris* and *Cyclosorus gongylodes*, but in the other two species some of the hairs, in various positions, are variously branched; the distribution of the hairs varies in detail among the four species (e.g., whether an acicular hair is present on stalk or body of sporangia).

Unicellular glandular hairs, sessile or stalked, on all parts as above. These vary considerably in their distribution in the four species; the presence or absence of a hair on stalk or body of sporangia may be significant (it is so in more than one species-group of this family in the Old World which I have examined).

Hairs of two or more cells, ending in a glandular cell. The distribution of these also varies considerably in detail in the four species. These hairs have the form of scales which are at an early stage of development, and may well be regarded as equivalent to scales; there is in fact not a sharp distinction between scales and the larger hairs of this type, in these and in other species of the family which I have examined. Such multicellular hairs may also appear as marginal outgrowths from scales, especially near bases of scales.

Sporangia. The significant differences appear to be in the nature, presence or absence of glandular or acicular hairs on the stalk and body, as already mentioned.

Spores. *Ampelopteris prolifera* differs from all the others in having a smooth exine, but agrees with *Goniopteris obliterata* in its folded perine; *Cyclosorus gongylodes* agrees with *Thelypteris palustris* in having a densely spinulose exine and no perine. Spore characters thus look distinctive, but there are practical difficulties for a herbarium botanist in observing clearly the distinction of exine from perine.

Venation. In *Thelypteris palustris* the veins are all free and nearly all forked; in the other species at least the basal veins from adjacent costules join to form an excurrent vein, differences being in the number of other veins which also join and in the length of the sinus-membrane (these differences in venation are in part to be correlated with depth of lobing of the pinnae).

Anatomy of rhizome. The four species differ in presence, distribution, and character of cells of the ground tissue which have thickened walls (only in *Thelypteris palustris* are there no cells with thickened walls). These characters may be useful for correlative purposes, but a taxonomic monographer could hardly be expected to examine such details in all species from herbarium specimens, so that in practice it might not be possible to assert that the character is universal in species recognized by other characters as belonging to a genus.

Tracheids. There is some difference in the deposition and connections of helical and annular thickenings in protoxylem; this, however, would be even more difficult for a monographer to observe, and without observation in many species the value of these distinctions in characterization of genera could not be assured.

Gametophyte. Though the gametophyte of *Goniopteris obliterata* has not been observed, that of another *Goniopteris* has been found to bear stellate hairs comparable with those of the sporophyte; this character would separate *Goniopteris* from *Ampelopteris* if general in the former. In *Cyclosorus gongylodes* the germ filament sometimes ends in a hair; in *Ampelopteris prolifera* and *Thelypteris palustris* it does not. *T. palustris* differs from the other species in lacking peg-like outgrowths from cell-walls on old gametophytes. In no case are acicular hairs produced by the gametophytes.

Buds on fronds. These are present on *Ampelopteris prolifera* and *Goniopteris obliterata* but not on the other two species.

Chromosome number. *Thelypteris palustris* (both in Europe and N. America) has n = 35, all specimens examined being diploid; the three other species have 36 as base number. Plants of *Cyclosorus gongylodes* have been examined in Japan, New Zealand, Ceylon, and West Africa, in all cases diploid, but Walker (1966, p. 177) found a tetraploid in Jamaica. The only record for *Goniopteris obliterata* (Walker, 1966, p. 179, 205) is of an apogamous triploid. *Ampelopteris prolifera* has been several times examined in Ceylon and India, in all cases diploid.

Application of these facts to problems of classification

Thelypteris. Morton, Schelpe, Proctor, and others have included all species in the family in one genus. All modern authors agree that the family is a natural one, and *Thelypteris* is the oldest generic name. But for those who find the diversity in the family too great for inclusion of all species in one genus, the problem of delimiting *Thelypteris* arises. Ching recognized *Thelypteris*, in a narrow sense, as a distinct genus, but did little to characterize it (1963, p. 297). He specified only the following characters: no acicular hairs on upper surface of rachis and costae (but such hairs are in fact present), costa at most only slightly grooved on the upper surface (not a distinct character), and (in the key to genera on p. 293) veins free and forked (but in N. American specimens, regarded as representing a variety of *T. palustris*, most veins are simple; see Fernald, 1929).

There is probably no one single character by which a genus *Thelypteris*, in Ching's sense, can be distinguished from all other members of the family (even the chromosome number 35 is shared by two species of *Metathelypteris* Ching, which appears to me a natural genus) and this may be true also of other species-groups which might have the rank of genus. These groups need to be distinguished each by a combination of characters; I believe that natural groups can be so distinguished. The information given in the present paper by Sen and Mittra suggests that the following may be a combination of characters by which a natural genus *Thelypteris* may be recognized.

> Rhizome long-creeping, slender; cells of ground tissue of rhizome uniformly thin-walled; scales bearing marginal and superficial unbranched acicular hairs and glandular unicellular hairs; similar hairs variously present on the surface of various parts of the frond, including body and stalk of some sporangia; thin narrow to broad scales ± persistent on lower surface of costae; fronds simply pinnate, pinnae deeply lobed, lowest pinnae not or little smaller than those next above them; veins all free, simple or forked, apices of veins all running to edges of pinna-lobes; spores with spinulose exine and no perine; terminal cell of germ filament forming the apical meristem of gametophyte; older gametophytes lacking peg-like outgrowths from their cells.

Even omitting the character of slender long-creeping rhizome, the above assemblage of characters applies, so far as I know, only to the species *T. palustris* in the broad sense. Ching recognized the southern variety *squamigera* (Schlecht.), which occurs in South and South tropical Africa, S. India, a few high mountains in Sumatra and New Guinea, and New Zealand, as a distinct species, and this seems justifiable. But then the status of the other varieties recognized by Fernald (1929) needs to be considered (and with it problems of nomenclature indicated by Morton, 1967, p. 71). Ching added the species *Nephrodium griseum* Bak., based on a single specimen from southern India which lacks the base of the frond; the specimen has young sori which do not show sporangial characters clearly, nor spores. In its lack of glandular hairs and of reduced scales on lower surface of costae, its copious rather thick acicular hairs on costae, and its supramedial sori on mostly simple veins, this looks to me very like *T. ochthodes* (Kze) Ching; the chief peculiarity of it lies in the forking of some veins and some marginal teeth on lobes of pinnae (exaggerated in Beddome's plate, Ferns Brit. Ind. t. 335). The forking of the veins is very irregular, and looks like an abnormality. I do not think it is at all closely related to *T. palustris*.

Cyclosorus. This name, ignored for many years, was revived by Christensen and re-defined by him (1913, p. 174) with the status of a subgenus of *Dryopteris*. But Christensen dealt only with a rather small number (14) of tropical American species and even these are not very uniform. He distinguished them from his subgenus *Lastrea* (= *Thelypteris sensu* Ching, 1940) by their basal veins running to each side of a sinus-membrane, or uniting to form an excurrent vein running to the membrane, whereas in *Lastrea* the basal veins all run to the margins of the lobes. Also nearly all species of subg. *Cyclosorus sensu* C. Chr. have unreduced lower pinnae (in no case are abruptly reduced very small pinnae present), whereas lower pinnae are usually reduced in subg. *Lastrea sensu* C. Chr. in tropical America.

Ching and Copeland, however, applied the name *Cyclosorus*, with generic status, in the Old World only to species in which the basal veins unite; and in the Malayan region a majority of such species have small reduced basal pinnae, often many. The number of such Old World species is very much greater than those of the New World included in subg. *Cyclosorus* by Christensen. Clearly therefore a new and more precise definition is needed if the name *Cyclosorus*, with generic status, is to be clearly distinguished. Based on the type species *C. gongylodes*, a possible definition of the genus might be as follows:

> Rhizome at least in some cases long-creeping; scales bearing marginal and superficial acicular and glandular hairs; cells of ground tissue of rhizome with radial walls only thickened; fronds simply pinnate, pinnae lobed, basal pinnae not reduced; basal veins from adjacent costules joining to form an excurrent vein which runs into the sinus-membrane, the next pair of veins either joining the excurrent vein or touching the sides of the membrane, the rest running to the edge of a pinna-lobe; some thin, broad, flat scales like those of the rhizome but smaller occurring on lower surface of costae; spherical glandular cells present (sessile) on lower surface of veins and at the ends of hairs on the stalks of some sporangia, *not* on the body of sporangia; spores with a densely and irregularly spinulose exine and no perine; gametophyte bearing peg-like outgrowths from its cells but lacking acicular hairs.

So far as I know, such a combination of characters applies only to *C. gongylodes* and to the closely allied *C. striatus* (Schum.) Ching on mountains of Africa. If the genus is to be extended to include other species, some of the characters will need to be removed from the above list, and then it will probably become difficult to characterize the genus in such a way as to distinguish it from other members of the family. In this connection, the following considerations are relevant.

The Old World species placed in the genus *Cyclosorus* by Ching and Copeland which agree with *C. gongylodes* in unreduced basal pinnae mostly have less deeply lobed pinnae and more than one pair of anastomosing veins. Where sessile spherical glands are present on the surface [a minority of cases in this group, one being *C. glandulosus* (Bl.) Ching] they are present also on the body of some or all sporangia; some other species, lacking glands on the surface, bear acicular hairs on the sporangia. Spores usually have a pronounced winged perine; where this is lacking, the spores do not have a densely and irregular spinulose exine.

The majority of species of Old World *Cyclosorus sensu* Ching & Copeland have rather numerous abruptly much-reduced basal pinnae, and a few of these (not all closely related) have prominent aerophores. There are, however, some species in which the basal pinnae are gradually reduced, the lowest not very small, and there are some in which basal reduced pinnae are few, irregular, and very small. These two intermediate groups of species appear to make difficult a sharp distinction between species with many much-reduced basal pinnae and those with none. One group of species which thus appears intermediate is that including *C. parasiticus* and *C. aridus* (Nayar & Chandra, 1963) and *C. molliusculus* (Kachroo, 1963); it also includes *C. dentatus* (Forsk.) Ching, type species of *Thelypteris* subg. *Cyclosoriopsis* K. Iwats. (1964, p. 28). Iwatsuki's definition of this species-group needs greater precision, which I believe can be obtained from sporangia and spores. In my experience, the basic characters of this group are: gradually but not excessively reduced lower pinnae; absence of spherical glandular cells on frond and on body of sporangia; presence on stalks of sporangia of elongate glandular cells (these occur also sometimes on lower surface of veins). The spores are also distinctive, as shown by Kachroo. Further, the presence of acicular hairs (Nayar & Chandra, Kachroo), sometimes of more than one cell, on gametohpytes, may be distinctive. These characters of spores and (so far as possible) gametophytes need to be clearly correlated with characters of glands and frond-form in all species before the group can be clearly delimited. The above observations are based on my recent study of many species, but it is not yet completed. When *Cyclosoriopsis* is distinguished in this way, the separation of species with unreduced basal pinnae from those with some reduced ones becomes simpler, but is still not fully solved.

Thus the whole question of the delimitation of a natural genus *Cyclosorus* is a very complex one. It is necessary to examine in detail characters of scales, glandular hairs, sporangia, and spores of all species, and desirable to check in a number of species the anatomical and gametophytic characters. Only when this is done can a delimitation of species-groups be effective; and only when the groups are delimited can one discuss possible inter-relations and the status of groups as genera, subgenera, or sections. I am now attempting a survey of this kind in the Malayan region and the Pacific (though I cannot study gametophytes), referring also to species of mainland Asia. Africa also has to be considered, and some examination of tropical American species is also necessary, to see how far any of them belong to groups defined in the Old World. My impression is that in the New World only *C. gongylodes* and some species of *Thelypteris* subg. *Cyclosoriopsis* Iwatsuki belong to species-groups also represented in the Old World.

Ampelopteris prolifera. The question here is whether the species should rank as a separate genus (as in Copeland, 1947) or be included either in *Goniopteris* or *Cyclosorus* (in most characters it differs so sharply from *Thelypteris palustris* that such differences need not be enumerated).

A. prolifera agrees with *Goniopteris obliterata* in (a) the presence of buds on the rachis, (b) the presence of branched unicellular hairs on parts of the frond, (c) exindusiate sori, (d) spores with a hyaline folded perine. In all these it differs from *Cyclosorus gongylodes.* It differs from *Goniopteris obliterata* in (a) the absence of branched hairs on the gametophyte, (b) presence of broad flat scales on lower surface of costa, (c) presence of large glandular cells at ends of hairs on sporangium-stalks (those of *Goniopteris obliterata* are much smaller), (d) the smooth exine of the spores. In all these, except the last, it agrees with *Cyclosorus gongylodes.* In the thickenings of the walls of ground tissue of the rhizome, and in the smooth exine of its spores, it differs from both *Cyclosorus gongylodes* and *Goniopteris obliterata.*

A. prolifera thus has characters in common with both *Cyclosorus gongylodes* and with *Goniopteris obliterata,* and in some it differs from both. As regards its differences from *Cyclosorus gongylodes,* it differs also from all other Thelypteroid ferns of the Old World in the branched unicellular hairs on the frond; and the only other Old World species which have proliferous fronds [*Cyclosorus cuspidatus* (Bl.) Copel. and a few allies in Malesia, *Cyclosorus pauciflorus* Ching, *C. blastophorus* Alston, and *C. patens* (Fée) Copel. in Africa] do not have sterile fronds of indefinite growth nor large glands on sporangium-stalks. As regards its differences from *Goniopteris obliterata,* one must remember that the latter, though closely allied to the type species of *Goniopteris,* is only one member of a fairly large genus (as defined by Christensen), not all species of which have been so closely scrutinized as *G. obliterata* in the present paper; and Morton (1963, p. 151) does not believe that the genus has yet been clearly defined. So a firm decision on the status of *A. prolifera* ought to wait on a clearer characterization of *Goniopteris.* But unless examination of other species of *Goniopteris* in the New World indicates that some of them agree fully with *A. prolifera* in the characters in which it differs from *G. obliterata, A. prolifera* may reasonably be regarded as having generic rank. I regard it as sufficiently distinct from all other Thelypteroid ferns of the Old World, and therefore rank it as a distinct monotypic genus pending clarification of its further possible relationships with New World species.

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