MORPHOLOGY OF THE EDIBLE FERN
AMPELOPTERIS KUNZE

By Prakash Chandra and B. K. Nayar

(*National Botanic Gardens, Lucknow*)

Abstract

Morphology of the sporophyte and gametophyte of *Ampelopteris prolifera* is described. The rhizome is dichotomously branched, short creeping and nearly naked except at the apex where it bears small basally attached, gland-tipped paleae bearing deciduous acicular as well as glandular marginal hairs. The parenchymatous ground tissue includes a few scattered partially thick-walled cells. The vascular cylinder is a radio-symmetric dictyostele dissected into narrow meristeles by spirally disposed leaf gaps, each associated with a pair of ribbon-like leaf trace bundles. Leaves are pinnate; most vegetative leaves on adult plants grow indefinitely and proliferate profusely by means of vegetative buds borne in the axils of some of the pinnae. The vascular connection to the bud is fused with that of the associated pinna and originates as a hollow cylindrical extra-marginal strand from the rachis bundle. The stipes (when young) and rachis bear characteristic, branched, unicellular, club-shaped hairs; elongated acicular hairs are found on the veins and on young lamina. Venation is goniopteroid. Sori are exindusiate, elongated and borne on the secondary veins. The sporangium is leptosporangiate and commonly bears 1 or 2 large glandular hairs on the stalk. The spores are bilateral, with smooth exine and granulose perine. On spore germination a uniseriate germ filament is produced, which develops into a cordate prothallus by forming a wedge-shaped meristematic cell in its terminal cell. The mature prothallus is cordate, with a thin midrib and broad wings. Young prothalli are naked. Aspidiaceous hairs are produced on the surfaces and margin towards maturity; sparse unicellular acicular hairs are often found on the margin of the mature prothallus. Sex-organs are of the common leptosporangiate type. It is concluded that *Ampelopteris* is closely related to *Cyclosorus* and that its separation as a genus from *Goniopteris* does not seem to be justified.

25

INTRODUCTION

Ampelopteris Kunze is a monotypic terrestrial genus of thelypteridoid ferns, widely distributed in India in the plains. It is abundant in N-E. India, where the young fronds are commonly sold in the market as a green vegetable. *A. prolifera* (Retz.) Copel. is a large fern of wet open places forming colonies covering extensive areas. It is particularly abundant in moist sandy soil, on the banks of rivers and streams, and grows even in areas which are seasonally submerged. It is a hardy fern, easy to propagate vegetatively and tolerant to a wide range of soil conditions, so that it can successfully be made a garden plant. Its peculiar, low growing, spreading habit makes it particularly suitable as an ornamental to cover ugly bare areas which develop in deep shade of perennial garden plants such as flowering trees, etc. With a sufficient supply of moisture and little care, *A. prolifera* forms an elegant green carpet of spreading finely dissected leaves covering quite extensive areas. Also, the young tips of fronds, which continuously grow and profusely proliferate can be successively plucked and used as a green vegetable.

Material for the present study is collected from the plains of Assam and cultivated in the fernery of the National Botanic Gardens. Spore morphology is studied from acetolysed preparations mounted in glycerine jelly (Erdtman, 1952). Prothalli were raised in the laboratory from spore cultures on sterile nutrient agar slants maintained at $24 \pm 2°$ C and at *ca*. 600 ft-c. light intensity (Nayar, 1962). The spore slides as well as herbarium vouchers of the material used in this study are deposited in the National Botanic Gardens, Lucknow.
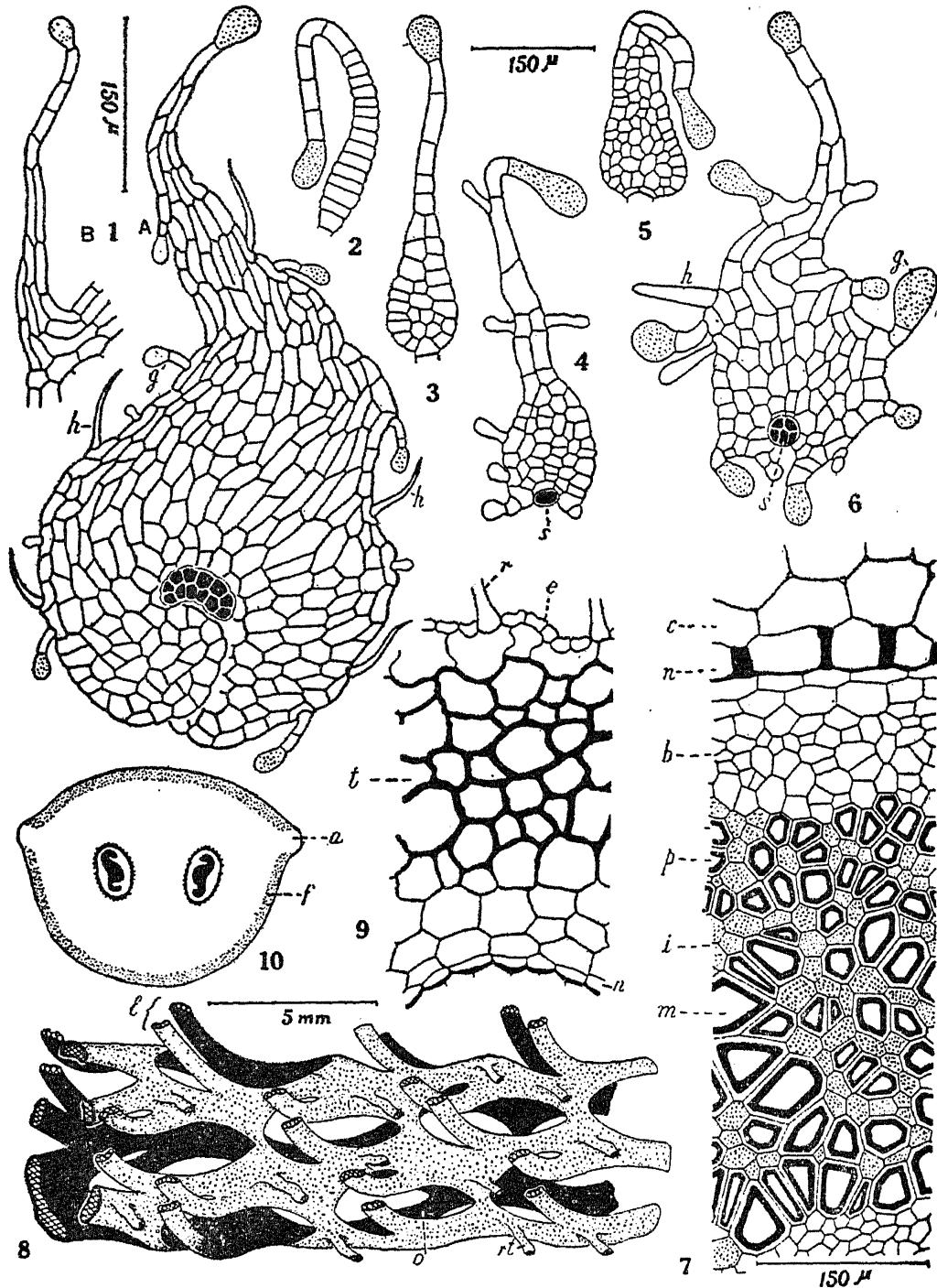
OBSERVATIONS

Rhizome

The rhizome of *A. prolifera* is creeping, sparsely branched, up to a centimetre across and often sub-epigeal. It is soft and blackish in fresh material. Branching is of the dichotomous type, with the branches nearly equal in size and divergent (often placed nearly at right angles to the main rhizome). Chaffy, ovate, thin-walled, small paleae cover the rhizome at the growing apex; paleae are sparse or nearly absent on the older regions. The paleae are basally attached by a ribbon-like short stalk. The basal region on either side of the stalk forms expanded auricles which overlap and mask the stalk, making the paleae pseudopeltate (Fig. 1 A). The anterior region of the paleae is gradually narrowed to an acute, uniseriate apex terminated

by a swollen club-shaped glandular cell. Both glandular and non-glandular hairs are profuse on the margins, but are usually shed at maturity so that the mature paleae are nearly naked. The non-glandular hairs (Fig. 1 A, *h*) are unicellular, elongated, slender, thick-walled, acicular and nearly devoid of contents. The glandular hairs (Fig. 1 A, *g*) are thin-walled, with dense cytoplasmic contents and may either be unicellular and papillate or with a swollen glandular cell supported on a slender, 1-4 cells long stalk. Rarely in some paleae one or two of these hairs towards the base are very prominent, and the basal region of their stalk may become multiseriate ; such hairs resemble the apical region of the palea (Fig. 1 B). The paleae originate as uniseriate slender hair-like appendages, several cells long and composed of short discoid cells. Cells at the distal end of the appendage elongate during development and the terminal cell becomes prominently swollen (Fig. 2), acquiring dense hyaline contents. Soon the cells towards the base (except the basal stalk cell) broaden and by repeated divisions form the expanded ovate-lanceolate body of the palea (Figs. 3-6). The basal cell develops into a pleuricellular narrow short stalk (Fig. 6). Marginal hairs are commonly formed when the body of the palea is 4 or 5 cells broad (Fig. 4), and develop from small lens-shaped superficial initials cut off from the marginal cells. Rarely hair formation is delayed till the paleae are over 10 cells broad (Fig. 5).

The ground tissue of the rhizome is parenchymatous with the cells having slightly thickened light-brown walls and dense deposits of starch grains. Scattered among the parenchyma are slightly elongated cells, usually with their wall on one side thickened and dark brown in colour. These cells recall the scattered sclerenchyma strands found in the rhizome of many of the aspidiaceous and thelypteridaceous ferns. The epidermal and one or two layers of hypodermal cells of the rhizome are thin-walled and devoid of any starch. A sheath of cells consisting of 5-7 layers next to the hypodermal cells are narrower than the other cells of the ground tissue and possess faintly thickened walls. The vascular cylinder of the rhizome is a radio-symmetric dictyostele, dissected into many narrow ribbon-like meristeles by closely placed large leaf gaps arranged in two or three closely placed spirals all around (Fig. 8). The meristeles are composed of a central massive band of xylem surrounded by a thin layer of phloem tissue, a one cell thick pericycle and an endodermal sheath composed of a single layer of cells with their radial and inner walls thickened. The xylem tissue is spongy on account of the several narrow plate-like groups of xylem parenchyma cells interspersed among the tracheids (Fig. 7). The leaf gaps are obovate in shape and each associated with a pair of narrow ribbon-like leaf trace bundles,

one on either margin nearly midway between the two ends of the gap. The anterior half of the leaf gap, beyond the leaf trace bundles, is conspicuously wider than the posterior half.

Figs. 1–10

Root traces are borne as slender superficial branches on the meristeles and are not associated with leaf traces. The roots of *A. prolifera* are soft, thick and sparsely branched. The central vascular strand of the root has a diarch ribbon-like xylem, with phloem restricted to either of its flat sur-

faces and surrounded by a pericycle and endodermis both of which are composed of a single layer of cells each. The inner layers of cortical cells of the root are thin-walled and parenchymatous (Fig. 9) ; the outer cortex (except one or two layers of hypodermal cells) consists of rather thick-walled dark brown cells. The piliferous and the hypodermal cells are thin-walled and parenchymatus.

Leaf

Leaves are borne in three or four closely placed spirals on the rhizome ; those on the ventral side are slightly displaced laterally. The stipe is non-articulated, glabrous, with a dark brown to blackish base and greenish upwards. Young stipes are copper-red in colour and covered by thin fugaceous paleae. The adaxial side of the stipe bears a broad median longitudinal groove. The vascular supply of the stipe consists of a pair of ribbon-like vascular strands (Fig. 10), structurally similar to the mcristeles of the rhizome but with the xylem band having thin recurved margins. The ground tissue is parenchymatous, but the epidermis and 6-8 layers of hypodermal cells possess slightly thickened walls. A broad, ill-differentiated band of aerenchyma tissue interrupt this peripheral sheath of thick-walled cells on either side (Fig. 10, *a*).

The leaf lamina is pinnate, the rachis bearing rather loosely placed simple sessile pinnae alternately on either side and bearing a similar or slightly larger terminal pinna. However, most of the vegetative leaves on the adult plants lack any terminal pinna and are of indefinite growth. Leaves of definite growth are erect or nearly so whereas those of indefinite growth are spreading, their flabellate anterior region often trailing over the substratum for long distances. These leaves persist for several seasons, elongating continuously and producing successive crops of daughter plants. Pinnae produced on the creeping terminal region are small, auricle-like and sparse on the rachis. The larger pinnae are oblong-lanceolate in shape, with a nearly truncate base, acute apex and bluntly lobed margin ; the larger ones are 10-15 (up to 20) cm. × 1-2 cm. The midrib of the pinna is grooved on the dorsal surface ; the groove is interrupted at the base and is thus not connected to the dorsal groove on the rachis. Venation is of the typical goniopteroid type (Fig. 16). The midrib has several pairs of nearly parallel lateral veins bearing obliquely placed simple secondary veins on either side. The secondary veins unite in pairs forming a series of angular areoles which are medianly divided by tertiary veins given off from the point where the secondary veins unite; each tertiary vein fuses with the secondary vein next

in succession on the basiscopic side. Two or three pairs of the secondary veins towards the tip of each lateral vein merge with the cartilagenous margin of the lamina instead of forming areoles like the others. The leaf lamina is thin and herbaceous, with the veins slightly raised on both surfaces. The mesophyll consists of three or four layers of prominently armed, densely chlorophyllous, parenchyma cells. The epidermal cells are chlorophyllous, thin-walled and with sinuous contour. The margin of the pinnae is composed of one or two rows of non-chlorophyllous, slightly thick-walled, large cells elongated parallel to the long axis of the pinna (Fig. 11).

A characteristic feature of *Ampelopteris* is the presence of vegetative buds in the axils of pinnae borne at irregular intervals on the rachis. These vegetative buds usually bear 2–4 small, erect, pinnate leaves during the first season, and later mostly strike root and develop into daughter plants. Successive buds are borne on opposite sides of the rachis and generally 6–12 "barren" pinnae are found between successive bud-associated pinnae on the same side of the rachis. The vascular connection to each pinna is a solitary gutter-shaped vascular strand originating extramarginally from the vascular strand of the rachis (Fig. 15, p_2). In the case of bud-associated pinnae the vascular connection to the pinna and its associated bud originate together as a large siphonostelic extramarginal strand. Soon after origin the pinna trace separates from the bud trace as a solitary gutter-like strand devoid of any associated gaps (Fig. 15, p_1). The siphonostelic vascular cylinder of the bud becomes dictyostelic upwards by developing spirally arranged leaf gaps as in the main rhizome. The first leaf of the bud is borne in the axil of the parent pinna. All leaves are supplied by paired vascular strands (Fig. 15, l) and are associated with prominent leaf gaps as in the main rhizome. An extra lacuna on the dorsal surface near the base of the bud trace is often found.
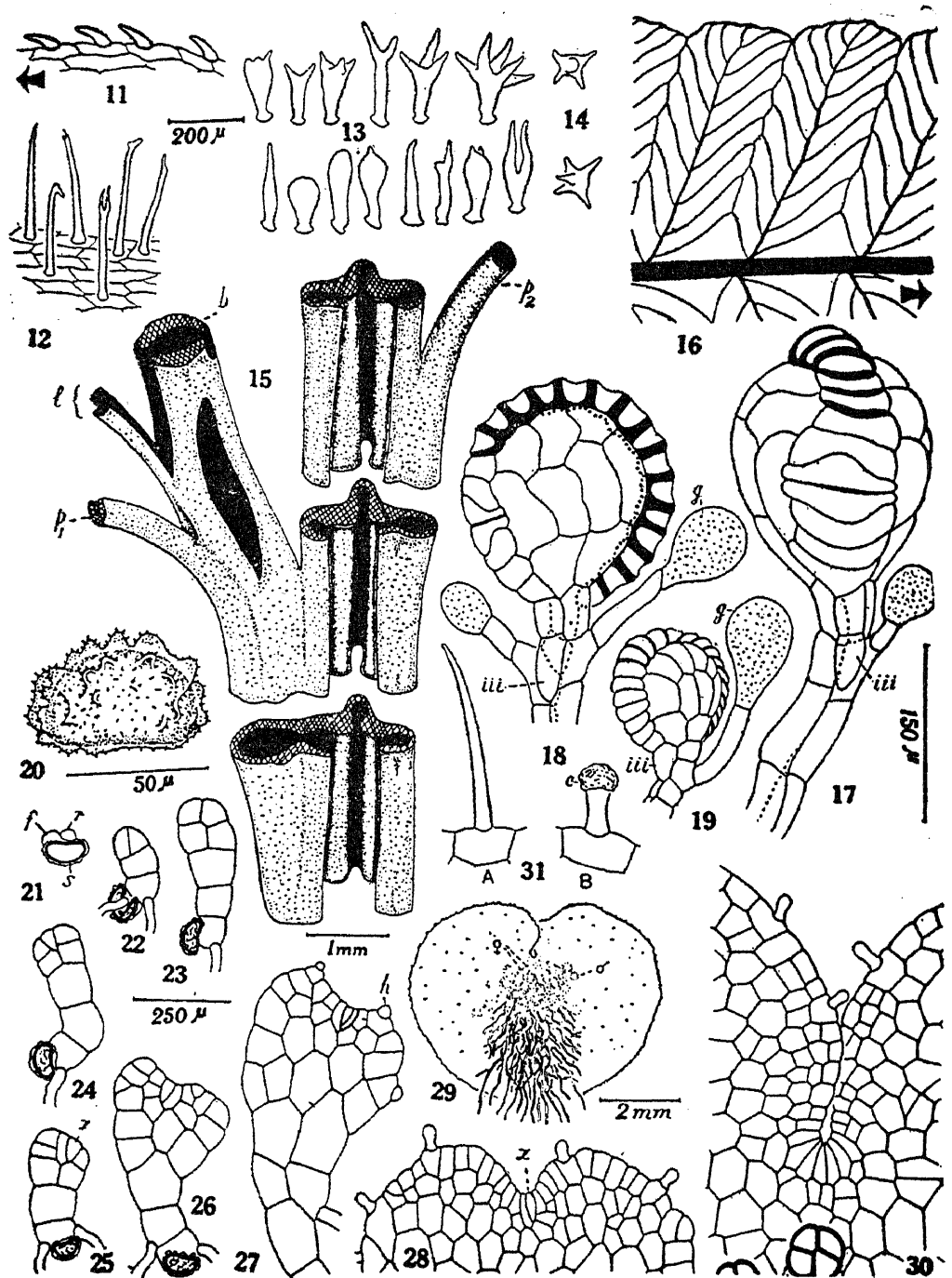
Typical unicellular hairs are borne on the rachis, veins and the cartilagenous margin of the leaf lamina. On the leaf margin they are short, acicular, spine-like and curved towards the apex of the pinna (Fig. 11). Slender acicular hairs are borne on the young lamina, but these are shed towards maturity. Hairs on the midrib (Fig. 12) and veins are slender, elongated and acicular ; the tip of some of these hairs is forked. On the rachis the hairs are short, stout and club-shaped, with the swollen anterior end bearing a few horn-like or spine-like branches (Fig. 13). Many of them bear 3–5 or more branches: viewed from the top these hairs appear star-like (Fig. 14). However, some are unbranched and a few balloon-like. Rarely some hairs are acicular or nearly so. All hairs are thin-walled, with

scanty protoplasmic contents and non-chlorophyllous. Hairs, similar to those on the rachis, are found on the young stipe also.

Sporangium and Spore

Fertile leaves are similar to the sterile ones, except that they are invariably of definite growth and crowned by a terminal pinna. The sorus is exindusiate, borne restricted to the secondary veins of the lamina and elongated along the vein, sometimes extending along its entire length. The sori are nearly covered when young by large yellowish glandular hairs borne on the sporangial stalks. Paraphyses are absent. The sporangium (Figs. 17, 18) is of the common leptosporangiate type, with a slender elongated stalk and lens-shaped capsule. The stalk is three or four cells long and is two cells thick, except at the capsule base where there is a short 3rd row (2 cells long) formed secondarily during sporangial development as reported in many leptosporangiate ferns. The two primary rows of stalk cells are contiguous with the flat lateral sides of the capsule, and the short 3rd row develops as a downward protrusion of the basal cell of the stomium. A large glandular hair is usually borne on the second cell (from the capsule base) of either one or both of the primary rows of stalk cells. Rarely hairs may even be found on the 3rd cell from the capsule base. Hairs, however, may be totally absent on some sporangia. The hairs are formed very early during sporangial development and are often longer than the developing sporangial capsule (Fig. 19), affording effective protection for the young sporangia. Each hair usually consists of a large, balloon-like, thin-walled terminal cell and a slender, elongated, usually one (rarely two) celled stalk. The terminal cell of the young hair contains dense, hyaline, cytoplasmic contents ; these later turn yellowish-brown. The annular ring of the sporangial capsule is vertical and interrupted by the stalk. Nearly 15 or 16 cells of this ring on one side possess highly indurated inner and radial walls ; the others constitute the stomium, of which a pair of cells at the middle is conspicuously broader (lip cells). Very rarely a sessile, balloon-like glandular hair may be borne on one of the indurated cells of the annular ring.

The spores of *A. prolifera* (Fig. 20) are of the bilateral type (Nayar and Devi, 1964 ; Devi, 1966), possessing a smooth, *ca.* $2\,\mu$ thick exine enveloped by a thin, light-brown, densely spinulose perine. The perine is loose except on the proximal surface, and wrinkled into sparse, short, thin, lobate or angular folds (*ca.* $5\,\mu$ tall from the exine surface). On an average the spores are $20 \times 30\,\mu$ (P $\times$ E, exclusive of perine) in size, but swells to $26 \times 47\,\mu$ when acetolysed.

FIGS. 11–31

Prothallus

On sowing, the spores germinate in *ca.* 6 days. The nucleus of the spore divides into a proximal (towards the laesura) smaller daughter nucleus and a distal (away from laesura) larger daughter nucleus. The former is soon cut off to form a lens-shaped, non-chlorophyllous, rhizoid initial cell next to the proximal pole of the spore (Fig. 21). The distal cell becomes

densely chlorophyllous and enlarges, opening up the laesural aperture and tearing apart the perine cover. It protrudes as a thick germ papilla through the aperture, pushing the rhizoid initial to one side. The rhizoid initial meanwhile elongates to form the first rhizoid. The germ papilla elongates and, by a series of transverse divisions, grows into a uniseriate, elongated, germ filament. Formation of a prothallial plate is initiated within a week of spore germination, when the germ filaments are 4–6 cells long. The terminal cell divides longitudinally (Fig. 22), commonly followed by the penultimate cell (Fig. 23). Soon an obconical meristematic cell is established in one of the daughter cells of the terminal cell by two oblique divisions nearly perpendicular to each other (Figs. 24, 25). By its activity the anterior region of the prothallial plate expands, becoming dorsiventral and spatulate (Fig. 26). The basal half of the germ filament, consisting of 2–4 cells, remains uniseriate and may produce one or two rhizoids.

The apex of the prothallus becomes notched nearly two weeks after spore germination (Fig. 26), and later becomes cordate (Figs. 27, 28). Marginal papillate hairs begin to develop soon after the apex of the thallus becomes notched (when the apex is 7–10 cells broad). The hairs are unicellular, capped, and of the common aspidiaceous type (Nayar, 1960 *a*, *b*; Nayar and Kaur, 1963, 1964, 1966). Superficial rhizoids are developed when the prothalli are distinctly cordate. The meristematic cell is replaced by a pleuricellular meristem (Fig. 30) in the usual way when the prothalli are nearly three weeks old. Soon afterwards a median midrib is developed behind the meristem. Prothalli reach maturity in *ca.* 5 weeks after spore germination. The full-grown prothallus (Fig. 29), is cordate, broader than long and with a deeply notched apex, a narrow light median midrib and spreadout broad wings. Unicellular aspidiaceous hairs (Fig. 31 B) are borne all over the margin and both the surfaces. In addition, unicellular elongated non-chlorophyllous acicular hairs (Fig. 31 A), of the type reported in some species of *Cyclosorus* (Nayar and Chandra, 1965), occur sparsely on the margins. Sex-organs are borne on the lower surface of the midrib; the antheridia often spread on to the adjacent areas of the wings. They are of the common type found in the advanced leptosporangiates. The antheridium is subglobose, with the basal cell short and mostly funnel-like. The opercular cell is single and collapses at antheridial dehiscence. The archegonial neck is slender, elongated and curved away from the apex of the prothallus. The neck canal cell is binucleate and swollen towards the tip at maturity.

B3

DISCUSSION

Ampelopteris is accepted by pteridologists as a derivative of *Cyclosorus* (Copeland, 1947). It has long been included either in *Cyclosorus* (Christensen, 1932), or *Goniopteris* (Ching, 1936, 1940 ; Christensen, 1911) both of which genera it resembles in many taxonomic features. Copeland separated it from *Cyclosorus* "as its remarkable proliferation and ramification is so out of order" in that genus (Copeland, 1947; 144), and from *Goniopteris* because of its geographic distribution (*Goniopteris* being exclusively American) and lack of branched unicellular hairs on the fronds, etc., which is characteristic of *Goniopteris*. The genus is recognised as a separate entity by Holttum (1954) and other contemporary pteridologists. Contrary to Copeland's contention, *A. prolifera* does bear branched, unicellular hairs with stellate heads, though on the leaf lamina these shade off into acicular hairs of the type typical of the thelypteridoid ferns. Holttum (1954) reported that branched hairs are totally absent in the Malayan specimens, but as he remarks, this species has only once been collected in Malaya (at Kinta River, by Dr. King's Collector). Since branched hairs are almost restricted to the stipe and rachis of *A. prolifera*, and these are deciduous, it is unlikely that they are preserved on old herbarium material. As such Holttum's observations on the Malayan material should not be taken as conclusive. Acicular hairs are found also on the paleae of *A. prolifera* (though sparsely) and the paleae are not naked as often described, but these paleal hairs are not branched or stellate as in *Goniopteris*. Thus, it seems difficult to separate *Ampelopteris* from *Goniopteris*, and the two genera agree in several characteristic morphological peculiarities like the proliferation of the fronds at the axils of the pinnae, the typical hairs on the rachis and exindusiate sori. Further similarities or dissimilarities, if any, cannot at present be judged since the morphology of the American *Goniopteris* is little known. However, the present taxonomic separation of the two genera seems open to question.

Morphologically *A. prolifera* agrees in all respects with the other thelypteridoid ferns like *Lastrea*, *Cyclosorus* and *Abacopteris*. The basally attached, gland-tipped paleae bearing non-glandular acicular hairs ; dictyostelic vascular cylinder of the rhizome, dissected entirely by the leaf gaps; leaf trace consisting of a pair of ribbon-like vascular strands; presence of non-glandular, unicellular, often acicular hairs on the frond; presence of spine-like hairs curved towards the apex of the pinnae on the cartilagenous margin of the lamina; sorus devoid of paraphyses; bilateral, perinate spores and cordate prothallus, developing aspidiaceous hairs towards maturity,

are characters they share. Several species of *Cyclosorus* (*C. aridus, C. gongylodes, C. papyraceous, C. parasiticus*), and some species of *Abacopteris* (*A. multilineata*) and *Lastrea* (*L. ciliata, L. erubescens*) bear glandular hairs on the sporangial stalk as in *A. prolifera*; some bear acicular and papillate hairs on the capsule wall, recalling the non-glandular often branched hairs on the sporangia of *Goniopteris*. A characteristic feature of the prothallus is the presence of at least a few acicular hairs on the margin at maturity. Such hairs are uncommon on fern prothalli and have so far been reported only in some species of *Cyclosorus* (*C. aridus, C. cuspidiatus, C. parasiticus*) and *Abacopteris* (*A. multilineata*) ; peculiar, branched, acicular hairs are reported in *Goniopteris* (Stokey, 1960). This, coupled with the mode of development of the prothallus (through the activity of an obconical meristematic cell formed in the terminal cell of the germ filament and the young prothallus devoid of any trichomes), indicates the close affinity of these genera to *Ampelopteris*.

REFERENCES

Ching, R. C.   .. "Revision of the Chinese and Sikkim Himalayan *Dryopteris* with reference to some species from neighbouring regions," *Bull. Fan. Mem. Inst. Biol.*, 1936, **8**, 157–268.

————   .. "On natural classification of the Polypodiaceae," *Sunyatsenia*, 1940, **5**, 201–68.

Christensen, C.   .. "On the genus *Dryopteris*," *Amer. Fern J.*, 1911, **1**, 33–37.

————   .. "The Pteridophyta of Madagascar," *Densk. Bot. Ark.*, 1932, Vol. 7.

Copeland, E. B.   .. *Genera Filicum*, Waltham, Mass., U.S.A., 1947.

Devi, S.   .. *Spore Morphology of Indian Ferns*, Ph.D. Thesis, Agra University, 1966.

Erdtman, G.   .. *Pollen Morphology and Plant Taxonomy*, Uppsala, Sweden, 1952.

Holttum, R. E.   .. *Flora of Malaya, Ferns*, Singapore, 1954, Vol. 2.

Nayar, B. K.   .. "Morphology of spores and prothalli of some species of the Polypodiaceae," *Bot. Gaz.*, 1962, **123**, 223–32.

————   .. "Morphology of the gametophyte of *Quercifilix* Copel," *Lloydia*, 1960 a, **23**, 102–08.

————   .. "The gametophyte and young sporophyte of *Athyrium esculentum* (Retz.) Copel," *Amer. Fern J.*, 1960 b, **50**, 194–203.

———— and Chandra, P.   .. "The gametophyte of some species of *Lastrea* Bory," *J. Indian bot. Soc.*, 1965, **44**, 84–94.

———— and Devi, S.   .. "Spore morphology of the Indian Ferns. 1. Aspidiaceae," *Grana palyn.*, 1964, **5**, 80–120.

Nayar, B. K. and Kaur, S.   ..   "Ferns of India. IX. *Peranema* and *Acrophorus*," *Bull.* bot. Gards., 1963, No. **81**, 1–40.

——————   ..   "Contributions to the morphology of *Tectaria*: The spo prothalli and juvenile sporophytes," *Bull. Torrey bot.* 1964, **91**, 95–105.

——————   ..   "On the fern genera *Acrophorus, Diacalpe, Lithostegia Peranema*," *Bot. Not.*, 1966, **119**, 1–23.

Stokey, A. G.   ..   "Multicellular and branched hairs on the fern gametophy *Amer. Fern J.*, 1960, **50**, 78–87.

EXPLANATION OF FIGURES

FIGS. 1–10. Fig. 1. Palea (A, fullgrown young palea; B, an unusually large basal marg hair on a young palea). Figs. 2–6. Stages in the development of palea. Fig. 7. T.s. of a tion of a meristele showing structure. Fig. 8. Vascular cylinder of a portion of the rhize Fig. 9. Portion of t.s. of the root cortex, showing thickening of cell walls. Fig. 10. T.s. of s (*a*, aerenchyma; *b*, phloem; *c, cortical cells*; *e*, piliferous layer; *f*, sheath of thick-walled c *g*, glandular hair; *h*, acicular hair; *i*, xylem parenchyma; *l*, leaf trace; *m*, metaxylem; *n*, e dermis; *o*, leaf gap; *p*, protoxylem; *r*, root hair; *s*, stalk; *t*, thick-walled cells of co *rt*, root trace).

FIGS. 11–31. Fig. 11. A portion of the cartilagenous margin of the pinna, sho spine-like hairs (the arrow points to the apex of the pinna). Fig 12. Epidermis ov portion of a lateral vein, showing hairs. Fig. 13. Hairs on the rachis, showing variations in f Fig. 14. Top view of two branched hairs, showing the star-like aspect. Fig. 15. Vascular c nization of portions of the rachis, showing vascular connection to a 'barren' pinna and a p associated with an axillary bud. Fig. 16. A portion of a pinna, showing venation (the a points to the apex of the pinna). Figs. 17, 18. Mature sporangia. Fig. 19. A young spc gium. Fig. 20. Lateral view of a spore. Fig. 21. Lateral view of a germinating spore, sho proximal rhizoid initial (*r*) and the germ papilla (*f*) lateral to it. Figs. 22–28. Stages ir development of the prothallus. Fig. 29. Adult prothallus, ventral view. Fig. 30. Ape mature prothallus, showing meristem and hairs. Fig. 31. Acicular (*A*) and papillate (*B*) thallial hairs. (*b*, vascular cylinder of bud; *c*, extracellular cap-like secretion; *f*, papilla; *g*, glandular hair; *h*, hair-initial; *l*, vascular connection to first leaf of the bud; p_1, cular connection to bud-associated pinna; p_2, vascular connection to "barren" pinna; *r*, rh initial; *s*, spore coat; *x*, meristematic cell; ♂, antheridium; ♀, archegonium; *iii*, the second developed, short row of stalk cells).