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GENUS *PRONEPHRIUM* PRESL IN INDIA

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ABSTRACT

In the present communication four new combinations of *Abacopteris* species under the name *Pronephrium* are proposed as the generic name *Abacopteris* Fée has been antedated by *Pronephrium* Presl (Holttum, 1971 ; Holttum and Chandra, 1971). The morphology of sporophyte and gametophyte of five Indian species of *Pronephrium viz. P. lakhimpurense, P. nudatum, P. penangianum, P. stenopodum* and *P. triphyllum* is also described.

INTRODUCTION

The genus *Pronephrium* Presl has recently been redefined by Holttum (1971). According to Holttum, 1971 ; Holttum and Chandra, 1971 ; the name *Pronephrium* Presl has priority over *Abacopteris* Fée. Also, he pointed out to the author (per. comm.) that according to Prof. C. V. Morton's latest investigations, the earliest name for *Abacopteris multilineata* (Wall.) Ching is *Polypodium nudatum* Roxb. As such the following new combinations are proposed for the Indian species:

Pronephrium lakhimpurense (Rosenst.) Holttum comb. nov. [basionym: *Dryopteris lakhimpurensis* Rosenst. Meded. Rijksherb. Leiden, 31: 7, 1917. Synonyms: *Dryopteris rubra Ching,* Bull. Fan. Mem. Inst. 2: 198, t. 12, 1931 ; *Abacopteris lakhimpurensis* (Rosenst.) Ching, Bull. Fan. Mem. Inst. 8:248, 1938].

P. nudatum (Roxb.) Chandra comb. nov. [Basionym: *Polypodium nudatum* Roxb., Calcutta Journ. Nat. Hist. 4: 491, 1844. Synonyms: *Polypodium multilineatum* Wall. ex Hook. Spec. Fil. 5: 11, 1863 ; *Goniopteris multilineata* (Wall.) Bedd. F.B.I. t. 231, 1867 ; *Abacopteris multilneata* (Wall.) Ching, Bull. Fan. Mem. Inst. 8: 253, 1938].

P. penangianum (Hook.) Chandra comb. nov. [Basionym : *Polypodium penangianum* Hook. Sp. Fil. 5 : 13, 1863. *Synonyms* : *Gymnopteris penangiana* Bedd. Fer. Brit. Ind. t. 232, 1867 ; *Abacopteris penangiana* (Hook.) Ching, Bull. Fan. Mem. Inst. 8: 255, 1938].

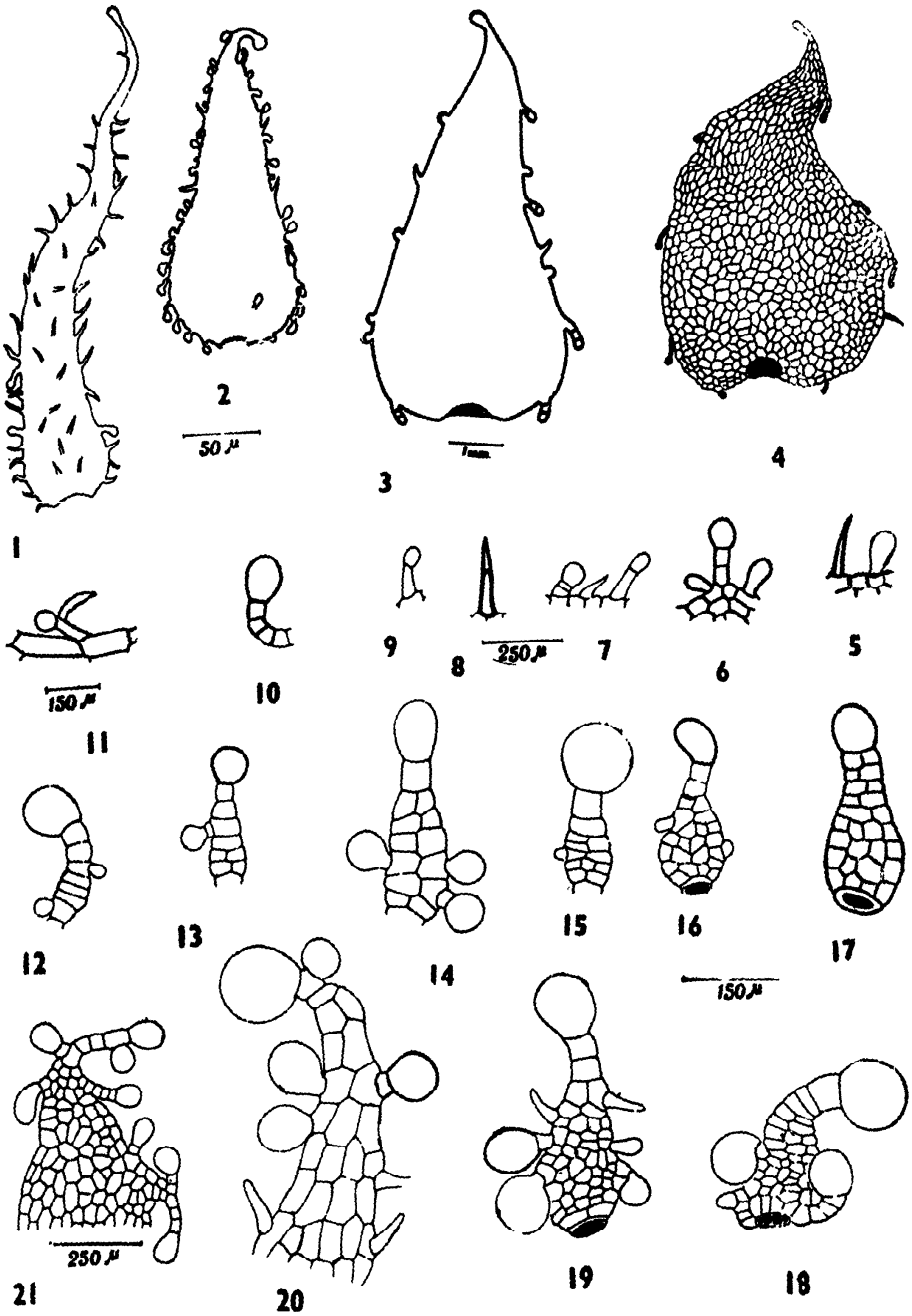
P. triphyllum (Sw.) Chandra comb. nov. [Basionym : *Meniscium triphyllum* Sw. Schard. J. Bot. 18002: 16. 1801. Synonym; *Abacopteris triphylla* (Sw.) Ching, Bull. Fan. Mem. Inst. 8: 241, 1938].

MATERIAL AND METHODS

The present study is based on 5 Indian species *viz. P. lakhimpurense, P. nudatum, P. penangianum, P. triphyllum* and *P. stenopodum.* All are terrestrial plants, occurring throughout the country up to an altitude of 2,000 metres, forming extensive colonies in deeply shaded, moist, humus-filled forest beds particularly near streams and water channels. *P. triphyllum,* however, forms small isolated patches (often between boulders) in semi-exposed, partially dry areas at the fringes of the forests.

The material was collected from the Khaṣhi & Jaintea Hill and North Cachar Hills of Assam and Mussoorie Hills. Spore morphology was studied from acetolysed preparations mounted in glycerine jelly. Morphology of prothalli is based entirely on cultures raised in the laboratory from the spores collected in the field. Cultures were maintained at a temperature range of 24 ± 2°C and light intensity of 600 ft. c.

Paleae : The paleae are basally attached, usually ovate-lanceolate in outline and terminated by a balloon-like glandular cell. A well defined stalk is absent, though in some species (*P. lakhimpurense,* Fig. 2 ; *P. stenopodum,* Fig. 3 ; *P. penangianum,* Fig. 4) a short clearly demarcated stalk is descernible in the larger paleae. In *P. penangianum* the base of the mature palea is prominently auriculate ; the auricles usually overlap each other making the palea pseudo-peltate. The paleae are profusely hairy (Figs. 5-10) ; the hairs are of three distinct types: (i) unicellular, acicular with thickened hyaline walls ; (ii) unicellular papillate (sometimes capped at the tip by wax-like extra-cellular secretion), and (iii) uniseriate, multicellular, terminated by a balloon-like terminal cell. The acicular hairs are profuse in *P. triphyllum* (Fig. 1) whereas in *P. penangianum* these hairs are



Figs. 1-21: 1-4. Mature palea of *P. triphyllum* (1), *P. stenopodum* (3), *P. penangianum* (4) and young palea of *P. lakhimpurense* (2). 5-7. Hairs on the palea of *P. nudatum*. 8. Septate acicular hair on the palea of *P. triphyllum*. 9-10. Hairs on the palea of *P. lakhimpurense*. 11. Hair on the plaea of *P. triphyllum*. 12-20. Stages in the development of palea. 21. Anterior region of the young palea of *P. lakhimpurense*.

rarely borne on the paleae. Occasionally, the acicular hairs are septate (Fig. 8) as in *P. stenopodum* and *P. triphyllum*. The papillate hairs are usually sparse in most of the species except in *P. lakhimpurense* where they occur profusely on the palea. The uniseriate, multicellular hairs are usually restricted to the basal region of the palea. Rarely, an acicular hair is borne on the stalk of the hair as in *P. triphyllum* (Fig. 11). The hairs are profuse on the young palea (Fig. 21) but are generally shed at maturity; in *P. lakhimpurense* the mature palea is nearly always devoid of hairs.

The palea originates as a uniseriate epidermal appendage (Fig. 12) close to the growing apex of the rhizome. Soon some of the cells of the appendage cut off small, lense-shaped hair initials laterally which develops into balloon-shaped glandular hairs. By repeated divisions of the intercalary cells and daughter cells, the body of the palea takes its ovate, sheild-like shape (Figs. 13-20). The basal cell remains uniseriate for some time, but eventually divides to form the narrow attachment region of the palea base.

Rhizome: The rhizome is usually short creeping, cylindrical and freely branched. It may be long creeping, 3 or 4 mm across, as in *P. triphyllum* or stouter as in *P. nudatum, P. penangianum, P. stenopodum* and *P. lakhimpurense*. Papillate, capped hairs (Fig. 22-p) mixed with the acicular ones (Fig. 22-k) are borne on the surface of the rhizome. The acicular hairs are usually unicellular but sometimes show transverse septum near the base as in *P. nudatum* and *P. triphyllum*. In addition glandular hairs (Fig. 22-t) with thin-walled, balloon-shaped terminal cell and a short, slender stalk, occur on the surface of the rhizome. In *P. nudatum* some of the glandular hairs (Fig. 23) are branched and each branch terminate in a globular secreting cell.

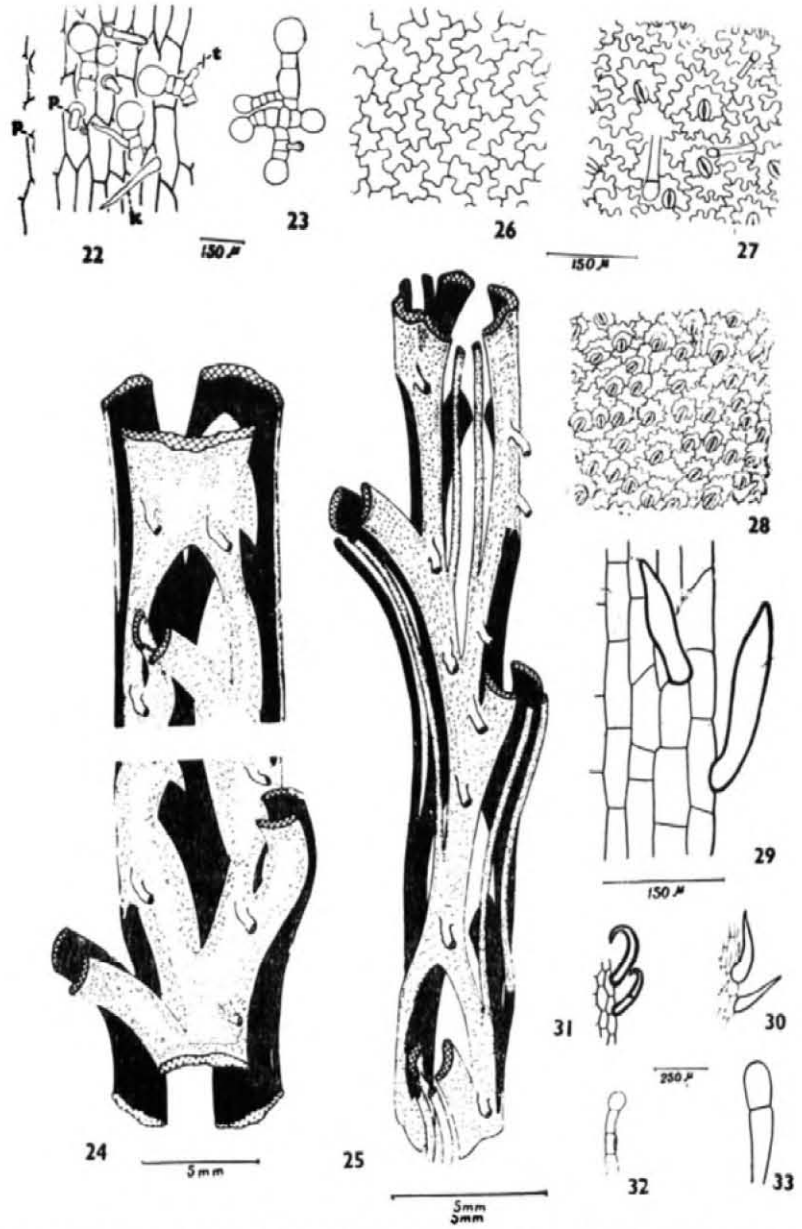
The ground tissue of the rhizome is parenchymatous with a peripheral sclerenchymatous sheath separating the outer cortex from the inner one. Slender, cylindrical strands of sclerenchyma are scattered in the ground tissue of the rhizome close to the stelar cylinder. These strands may be large (8-12 cells thick as in *P. triphyllum* and *P. penangianum*) or quite slender (usually 1-2 cells thick in *P. nudatum*). The cells of these strands are highly thick-walled with occluded lumina and appear to be associated with the departing leaf traces.

The vascular cylinder is a dictyostele, dissected by narrowly-ovate leaf gaps (Fig. 24) into 2-4 broad ribbon-like meristeles. The endodermal cells are slightly thick-walled and radially compressed; the thickening of the inner and the radial walls of these cells, which is found in many ferns, is absent here. The pericycle consists of two or three layers of large parenchymatous cells. The xylem tissue is ribbon-shaped and massive; it is composed of several layers of rather narrow tracheids interspersed with broad, thin, interconnected bands of small parenchyma cells (spongy xylem). The protoxylem is restricted to small groups at the periphery of the xylem bands. The phloem surrounds the xylem on all the sides.

Leaf: The leaves are spirally arranged and are often closely placed on the rhizome. The stipe is slightly swollen at the base and bears sparse unicellular, acicular hairs on the surface; sometimes the hairs are septate as in *P. triphyllum*. The vascular supply to the stipe consists of a pair of large, laterally placed, ribbon-like vascular strands, having a prominently incurved adaxial margin. In *P. lakhimpurense* the two vascular strands are split to the base by a longitudinal lacuna so that each leaf receives a pair of broad, ribbon-like adaxial bundles and a pair of narrow abaxials (Fig. 25). In all the species sclerenchyma strands occur scattered in the ground tissue at the base of the stipe. These strands tend to aggregate towards the centre of the stipe and are continuous with the sclerenchyma strands of the rhizome, ending blindly a little distance up the stipe. The rachis is similar to the stipe in structure. Towards the anterior half of the rachis the two vascular strands fuse together by their abaxial margins to form a solitary gutter-shaped bundle. Vascular connection to the lateral pinnae originate extramarginally from near the infolded adaxial margins of this vascular strand.

The pinnae are short stalked, broadly lanceolate and tending to be subfalcate. The veins are in several pairs and all are anastomosing. The lateral secondary veins unite regularly in pairs to form a series of angular areoles with an excurrent tertiary veinlet pointing away from the midrib. The tertiary veinlets are short and end blindly in *P. lakhimpurense* and *P. stenopodum*, whereas in *P. nudatum, P. penangianum* and *P. triphyllum* successive tertiary veinlets unite end to end forming a zig-zag continuous vein parallel to the primary veins. The lamina is thin and tough. The mesophyll is composed of densely chlorophyllous, armed parenchyma cells and is not differentiated into palisade and

spongy tissue. The anticlinal walls of cells of both the upper (Fig. 26) and lower epidermis are highly sinuous. Stomata are anomocytic and restricted to the lower epidermis and are often more than three-fourth encircled by one of the subsidiary cells (Figs. 27, 28).



Figs. 22-33: 22. A portion of rhizome epidermis of *P. nudatum* showing three types of hairs (p-papillate ; k-acicular ; t-glandular). 23. A large glandular hair on the rhizome of *P. nudatum*. 24-25. Vascular cylinder of a portion of rhizome of *P. nudatum* (24) and *P. lakhimpurense* (25). 26. Upper foliar epidermis of *P. lakhimpurense*. 27-28. Lower foliar epidermis of *P. lakhimpurense* (27) and *P. nudatum* (28). 29. Acicular hairs on the upper surface of the midrib of *P. penangianum*. 30-31. Acicular hairs on the leaf margin of *P. nudatum* (30) and *P. triphyllum* (31). 32-33. Hairs on the foliar epidermis of *P. nudatum* (32) and *P. stenopodum* (33).

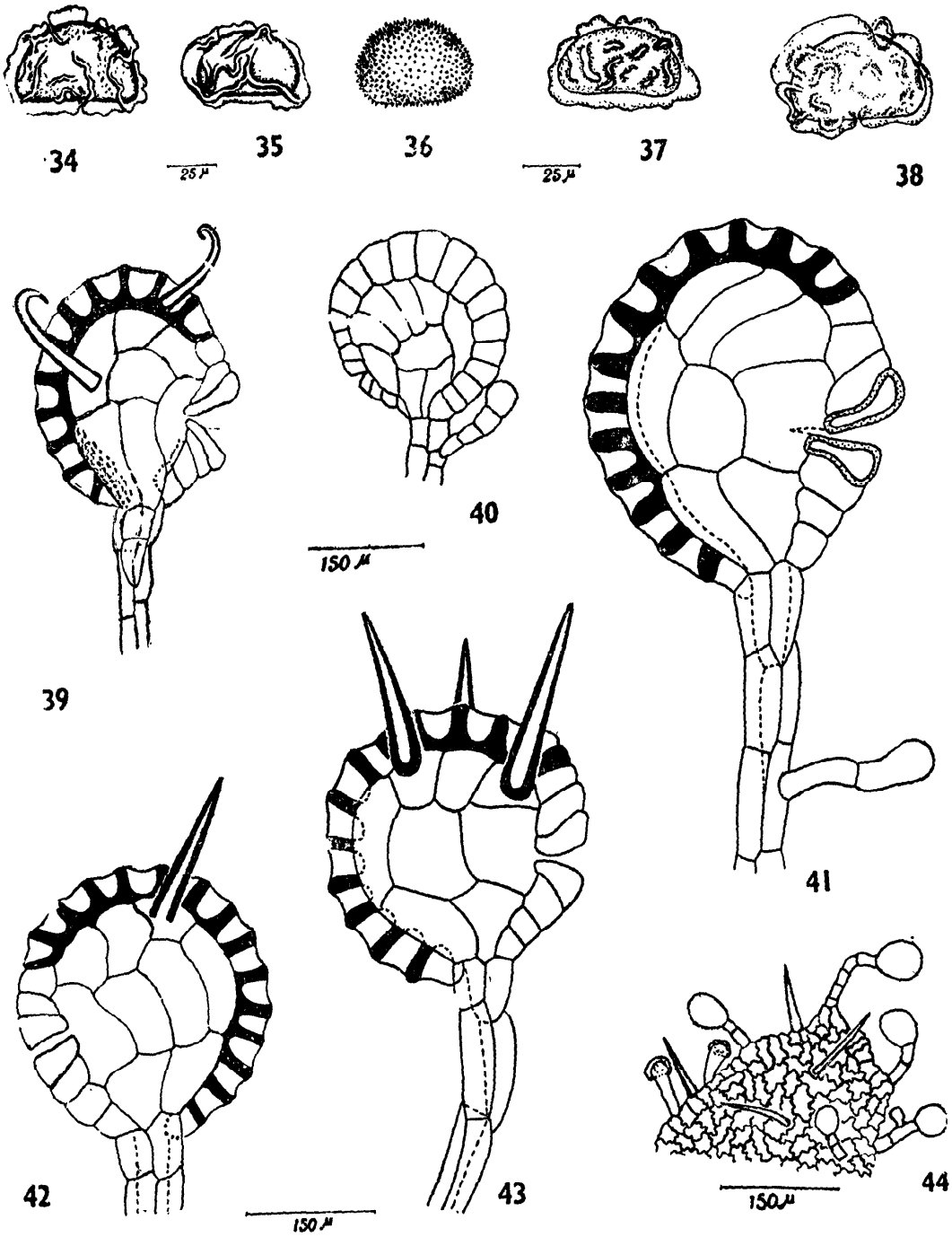
The leaf lamina bears all the three types of hairs described for the rhizome. The acicular hairs are dense on the midrib and the main veins. These hairs are either hooked (*P. triphyllum*) or short, slender and spine-like (*P. nudatum, P. stenopodum, P. lakhimpurense*). *P. penangianum* has stout, thick-walled, unicellular, acicular hairs on the upper surface of the midrib (Fig. 29); these hairs are similar to the hairs reported in *Ampelopteris prolifera* (Chandra and Nayar, 1968). In addition a few short, club-shaped glandular hairs (Fig. 33) also occur on the non-venous areas of the lower epidermis in *P. lakhimpurense* and *P. stenopodum*. In *P. nudatum* and *P. penangianum* the glandular hairs have longer stalk of 2-8 cells long (Fig. 32). The acicular hairs (Fig. 30) are borne on the margin of the pinnae in all the species except in *P. penangianum* where the margin is devoid of them. In some species like *P. triphyllum* the acicular hairs are thick-walled, occasionally septate and hooked; the hooks are directed towards the apex of the pinna (Fig. 31).

Sorus and sporangium: The sori are either superficial, circular (*P. nudatum, P. penangianum*) or located at the ends of secondary veins and are elongated along the veins (*P. lakhimpurense, P. triphyllum, P. stenopodum*). The sorus is exindusiate in *P. triphyllum, P. stenopodum* and *P. penangianum*. In *P. nudatum* the indusium is prominent, whereas in *P. lakhimpurense* it is fugaceous and lost early during development so that the sorus appears exindusiate. In *P. nudatum* the indusium is profusely hairy; the acicular hairs mixed with the multicellular glandular hairs and unicellular, capped hairs occur on the margin and surface of the indusium (Fig. 44).

The sporangium consists of a lens-shaped capsule borne on a slender stalk. The stalk of the mature sporangium is usually four cells long and two cells thick throughout except at the capsule base where there is an incomplete, short third row contiguous with the side of the capsule. In *P. nudatum* (Fig. 40), *P. penangianum* (Fig. 41) and *P. triphyllum* (Fig. 39) glandular hairs are often borne on the stalk of the sporangium. The capsule wall in *P. lakhimpurense* (Fig. 42) and *P. triphyllum* (Fig. 39) usually bears one or more thick-walled acicular hairs near the annulus.These hairs in *P. triphyllum* are usually hooked and in *P. lakhimpurense* sometimes septate. In *P. stenopodum* (Fig. 43), 1-3 (up to 5), long straight, unicellular, acicular hairs are borne on the capsule; occasionally these hairs are found on the annular cells of the sporangium. The capsule wall of *P. nudatum* and *P. penangianum* are devoid of acicular hairs. The annulus is generally 12-16 cells long and well differentiated.

Spores: The spores are bilateral, plano-convex to more or less concavo-convex in the lateral view. A distinct perine is found in all the species except *P. nudatum* (Fig. 36) in which the perine is absent. In *P. triphyllum* (Fig. 34) the perine is dark-brown in colour, faintly granulose and thrown into blunt, rugula-like folds protruding ca. 4 μ from the exine surface. The perine in *P. lakhimpurense* (Fig. 35) is nearly hyaline and faintly granulose. It is more or less loose and shows thin, irregular folds most of which are elongated parallel to E-I axis of the spore and protrude ca. 8 μ from the exine surface. In *P. penangianum* (Fig. 38) the perine is light brown in colour, rather loose and shows sinuous, sometimes semi-circular folds with smooth crest. The leasura is unthickened except in *P. triphyllum* in which the inner margin of the laesura is prominently thickened. The exine is brown in colour, and 1.5 μ (*P. triphyllum*) to 3.5 μ (*P. lakhimpurense*) thick. The exine in *P. nudatum* is densely spinulose; the spinules being sharp, brown in colour, ca. 2 μ long and ca. 1 μ broad at the base. In some species like *P. lakhimpurense, P. triphyllum* and *P. stenopodum* the exine is smooth. On an average the spores are ca. 24×38 μ (P × E, exclusive of perine) in size. In *P. stenopodum* the spores are slightly smaller in size (22×30 μ) with prominently granulose perine which is wrinkled into short flap-like folds (Fig. 37). The spores contain small, pale-yellow oil globules and dense chloroplasts.

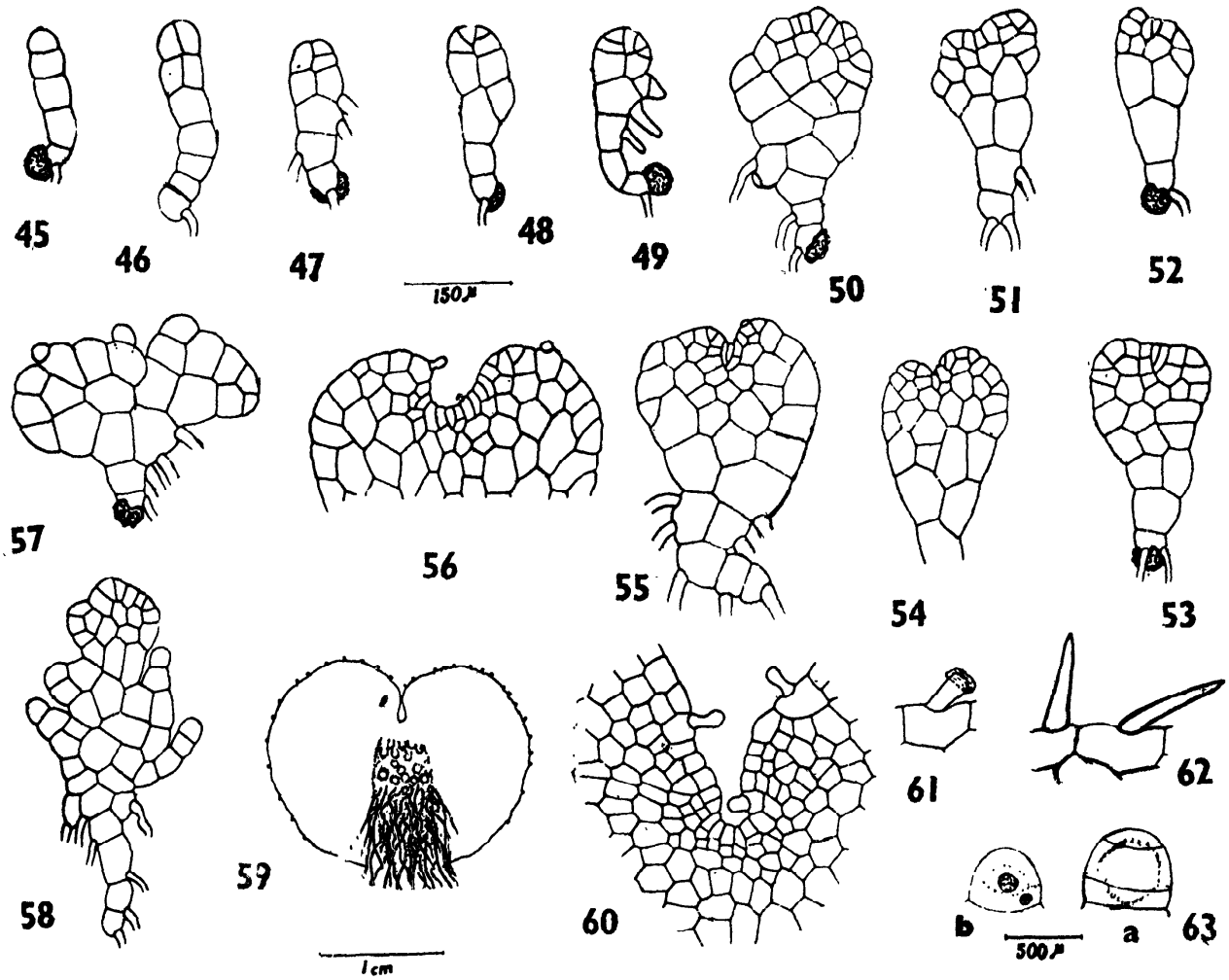
Prothallus: Spore germination is of the Vittaria-type (Nayar and Kaur, 1968). The formation of prothallial plate is initiated when the germ filaments are usually 3-6 cells long (Fig. 45). The terminal cell and the cell next to it divide longitudinally and the anterior end of the filament expands (Figs. 46-48). An obconical meristematic cell is soon established apically (Fig. 48) by two oblique divisions in one of the daughter cells of the terminal cell. In *P. triphyllum* and *P. lakhimpurense* the establishment of meristematic cell is often delayed (Figs. 49-51). In *P. nudatum* (Figs. 52, 54, 56) a meristematic cell is differentiated early and develops into a spatulate prothallial plate in about two weeks after spore germination. In *P. lakhimpurense* and *P. triphyllum* the prothallial plate generally become spatulate at the



Figs. 34-44: 34-38. Lateral view of the spores of *P. triphyllum* (34), *P. lakhimpurense* (35), *P. nudatum* (36), *P. stenopodum* (37) and *P. penangianum* (38). 39. Mature sporangium of *P. triphyllum*. 40. Young sporangium of *P. nudatum*. 41-43. Mature sporangia of *P. penangianum* (41), *P. lakhimpurense* (42) and *P. stenopodum* (43). 44. A portion of indusium of *P. nudatum*.

apex before apical meristematic cell is differentiated (Fig. 53). Many thalli, however, remain non-meristematic for a long time and in some cases the meristematic cell stage is omitted. The apical meristematic cell is replaced by pleuricellular meristem only after the thalli have become distinctly cordate (Figs. 56, 60). In *P. triphyllum* there is a tendency for the prothallial plate to develop irregular lobes (Figs. 57, 58). Such thalli remain non-meristic and develop into irregularly shaped plates which later bear antheridia and remain antheridial throughout. The prothalli become fully grown in about 3-4 months after the spore germination (Fig. 59). The mature prothallus is profusely hairy; the hairs being unicellular, papillate with a cap-like waxy secretion at the apex (Fig. 61). In *P. nudatum*, mixed with these, elongated, slighlty thick-walled acicular hairs (Fig. 62) are sparsely borne on the surface of the thallus. However, the young cordate prothalli in all the species are devoid of trichomes (Figs. 55, 56).

Sex organs are of the common type reported in



Figs. 45-63 : 45. Germ filament of *P. nudatum*. 46-47. Initiation of plate formation in the germ filament of *P. lakhimpurense* (46) and *P. triphyllum* (47). 48. Establishment of apical meristematic cell in the young prothallus of *P. nudatum*. 49-51. Non-meristic prothallial plate of *P. triphyllum* (49) and *P. lakhimpurense* (50-51). 52-53. Spatulate prothallial plates of *P. nudatum* (52) and *P. lakhimpurense* (53). 54-56. Young cordate prothallial plates of *P. nudatum* (54-56) and *P. triphyllum* (55). 57-58. Irregular non-meristic prothallus of *P. triphyllum* (57) and *P. lakhimpurense* (58). 59. Mature prothallus of *P. nudatum*. 60. Apical notch of the mature prothallus of *P. triphyllum*. 61-62. Marginal hairs on the mature prothallus of *P. nudatum*. 63a,b. Fully developed (63a) and young (63b) antheridia of *P. nudatum*.

the advanced leptosporangiate ferns. The antheridium is subglobose or hemispherical (Fig. 63 a, b) and has the same type of structure and development as reported in the higher ferns (Verma and Khullar, 1966). The structure and ontogeny of the archegonium are similar to those as reported in the leptosporangiate ferns (Stokey, 1951).

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