

MORPHOLOGY OF *PALLAVICINIA* WITH REFERENCE TO ITS
SPECIES PROBLEM AND THE INDIVIDUALITY OF
*PALLAVICINIACEAE*¹

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Pallavicinia with about 40 species is spread over tropics of both the hemispheres. Stephani (1900–24) divides it into two sections: Procumbentes (*Eupallavicinia*) and Dendroideae (*Mittenia*). In India it is represented by 7 species with restricted distribution (see Chopra, 1943).

The present investigation gives a morphological account of *P. ambigua* (Mitt.) St., *P. Lyellii* (Hook.) Gray and *P. longispina* St. The development of sex organs has been studied in detail in *P. ambigua* and *P. Lyellii*. In case of *P. longispina* a study of archegonium was made from herbarium specimens and the stages available do not suggest any marked deviation from the general plan for the genus. Since the development of sex organs follows the usual plan described for other Anacrogynous Jungermanniales it is thought desirable to omit the figures so common in literature. A study of variations of certain characters of thallus including the structure of antheridial scales (except in *P. longispina*, where male plants were not available), involucre and perianth has been undertaken in each species to determine their bearing on the species problem of the genus.

P. ambigua, collected from Travancore, India (through courtesy of Mr. S. Nayar, to whom thanks are due), grows along moist cuttings and sheds spores by the end of monsoons. During the unfavourable periods the thalli, as in other species of the genus, lose their wings except towards the growing tips, become thickened, hard and dark brown. These parts form the basal prostrate region while they resume growth and develop aerial assimilatory shoots. *P. Lyellii*, collected from various places from Assam and Japan (through courtesy of Dr. S. Hattori), is restricted to moist protected places adhering to stones or along banks of streams or on moist hill slopes. In Japan it also grows on soil rich in humus and epiphytically on bases of *Cryptomeria japonica* (Hattori, personal communication). *P. longispina* collected from various places in Japan (by Dr. S. Hattori) occurs on humus, exposed and moist rocks, fluffy banks, moist soil and stream banks.

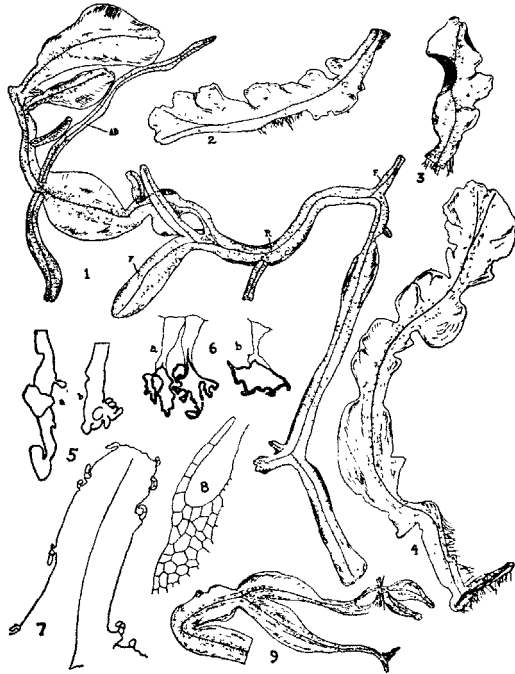
EXTERNAL FEATURES

The species are unisexual, occur in patches, are translucent pale to yellowish-green, simple or branched and prostrate as in *P. levieri* and *P. radiculosa*. *P. longispina* sometimes shows the habit (Fig. 10) exhibited by *P. zollingeri* (Smith, 1938). All species have an ascending, more or less flat, winged region and a basal wingless rhizomatous region (Fig. 1). The former have the margin entire, wavy, undulate or with indistinct or distinct leaf-like lobes (Figs. 2–4); and the latter is

¹ This investigation was carried out at Gauhati University, Assam, India.

formed by the suppression of the wings caused by non-availability of light or, due to their being covered by the ascending winged region, they serve to bring the latter into light. Rhizoids are borne only on the midrib region, unlike that in *P. leviseri* (Campbell, 1939) where they arise from the entire ventral surface. They harbour a number of unicellular and filamentous algae. In *P. Lyellii* often they are localized (Fig. 9) and the rest of the midrib lacks them. They are yellowish-light brown, long, thick walled, with sucker-like tips (Fig. 5), and in epiphytic forms shorter, with broad suckers (Fig. 6); and thin, long, without suckers—the former for fixation and the latter for absorption. The midrib shows a conspicuous mid-dorsal vein, becoming black with age, and with a broad one cell thick, longitudinal wing on its either side. The former consists of conducting tissue and the latter is entirely photosynthetic with cells, 4–6 angled, thin or nearly thickened.

The thalli in *P. ambigua* are up to 5 cm. long, 4–5 mm. broad, with the midrib region about 0.5–1.5 mm. broad and nearly convex on the ventral surface, when young bearing 1–3 cell long hairs (Fig. 7) along the thallus margin—more aggregated towards the apical notch, becoming stouter in the older regions and mostly drying up or decaying off due to low moisture; in *P. Lyellii* they are up to 7 cm. long, 5 mm. broad, with the mid-dorsal vein about 0.5 mm. broad and in *P. longispina* they are up to 5 cm. long, about 6 mm. broad, with the midrib region 0.5–1 mm. broad, occasionally indistinctly concave, the margin of the thallus bearing



Figs. 1–9.

- Fig. 1. *P. ambigua*, thallus with basal rhizomatous region (R), young adventitious branches (AD) and forkings (F). $\times 3\frac{1}{2}$.
 Figs. 2–4. Same showing thalli with lobes and leaf-like margins. $\times 3\frac{1}{2}$.
 Fig. 5. Apices of rhizoids in *P. ambigua* and *P. Lyellii*. $\times 100$.
 „ 6. Rhizoids of epiphytic forms of *P. longispina*. $\times 100$.
 „ 7. Apex of a lobe of *P. ambigua* showing marginal teeth. $\times 35$.
 „ 8. A marginal tooth from thallus of *P. longispina*. $\times 35$.
 „ 9. Thallus of *P. Lyellii* (note forking, walking habit and localization of rhizoids). $\times 3$.

3-6 cell long, persistent hairs or spines (Fig. 8)—more aggregated towards the apex, white to yellowish in colour and becoming light brown with age. The epidermal cells and the cells towards the middle of thallus are variable in size, even within the same species. In all the species studied here the surface cells of the vein are polygonal broad-linear, usually with highly thickened cells and about $45 \times 30\mu$ or $60 \times 18\mu$.

Forking of the thallus is caused by a vertical division in the apical cell. Such forkings may have a limited or unlimited growth, depending on the available light and moisture conditions. Often those developing archegonial receptacles may stop further growth. Adventitious branches are formed profusely as ventral innovations from the midrib region and in their formation there is not a forking of the apical cell; they are cylindrical to begin with but sooner or later develop wings, first around the apex. Usually the basal region retains the cylindrical form, distinctly or indistinctly. Each in turn develops one to many ventral innovations and a single plant may become as much as 7 cm. in diameter. It is, however, interesting to note that the first adventitious branch and those developed from it in turn are formed from the same side of the wings as that of the first branch from the thallus; in other words if the first adventitious branch is formed from the left side of the thallus, those developed from it in turn will also be formed from the left side of the respective branches bearing them.

Perennation and vegetative propagation: *P. Lyellii* and *P. longispina* perennate with help of apical tubers. The latter represent the swollen apices and are formed at the end of the growing season. They are cylindrical and profusely covered with thick-walled, pale pinkish-brown rhizoids (Fig. 11); usually underground or in the epiphytic forms burying themselves in the substratum formed by mosses. In *P. longispina* more than one may be formed per thallus and the plant may thus assume a 'walking habit' (Fig. 12; an occasional case figured for *P. Lyellii*, Fig. 9). In all the species perennation is also by the rhizomatous region which is dormant during unfavourable periods.

Vegetative propagation is mostly by fragmentation of adventitious branches, or of the basal rhizomatous region; in *P. longispina* also by formation of 'stolon-like' structures (Fig. 11) which are such adventitious branches that lose their wings, become cylindrical, long (up to 3 cm.), thick and have a somewhat burrowing habit. Later they develop wings along the apex.

INTERNAL STRUCTURE

The midrib of the thallus is usually about 10-11 cells thick in *P. ambigua*, 12-14 cells in *P. Lyellii* and 12-30 cells in *P. longispina*. It suddenly passes into the wings, one cell thick and with thin-walled polygonal cells. The central conducting region consists of long, narrow, thick-walled cells running parallel to the mid-dorsal vein, about 6μ wide and pitted as in other species of the genus (Campbell and Williams, 1914) and *Symphyogyna* (Finlayson, 1950). It serves for conduction of solutes and a branch from it may or may not be given to the female receptacle. It has no connexion with the conducting region of adventitious branches. It is, however, connected with the branches formed as a result of forking. Here it divides far in advance of the forking. The region below it is parenchymatous and in the older thalli infested with a mycorrhizic fungus; and becoming light brown together with the adjacent cells later on. The mycorrhizic fungus is inter- and intra-cellular (Fig. 13*b*) and enters the thallus through the rhizoids (Fig. 13*a*). It spreads in the cells just below the conducting strand and rarely in those towards the dorsal surface but never in the receptacles. They are neither symbiotic nor obligatory for the development of the thallus. The young adventitious branches lack them. The wingless rhizomatous region is nearly spherical in a cross-section and consists of parenchymatous polygonal cells, full of starch and fungal hyphae and with the

outer cells thick walled. In stolons such cells develop chloroplasts, are polygonal, thin walled and lack fungal hyphae when young.

Apical cell: The apical cell is lodged within the apical notch and is protected by a number of 3-5 celled hairs with mucilaginous tips (Fig. 14). It is two sided as in most of the other species of the genus (Campbell and Williams, 1914; Haupt, 1918), *Riccardia pinguis* (Clapp, 1912), *R. indica* (Kachroo, 1953), *Metzgeria himalayensis* (unpublished data) and *Hymenophyllum* (Goebel, 1905). It cuts off segments alternately right and left, each of which is cut into an inner cell and an outer cell—the former contributes to the thick midrib and the latter to the cells of the wing. Farmer (1894) reports an apical cell with 3 cutting faces in *P. decipiens*.

MALE PLANT

They are much narrower than the female plants in contrast to *P. radiculosa* where both are equal in size (Smith, 1938); usually about half in breadth and nearly equal in length; narrowly linear and short-lived. They may fork once or twice at the apex (Fig. 16). In *P. ambigua* often the midrib region is prolonged into a thin flagellum-like shoot with a bunch of rhizoids at the apex, probably serving for vegetative propagation (Fig. 15). Antheridia are borne on each side of the midrib either in continuous series or in series interrupted here and there by sterile areas. Each (Fig. 16) or a group of 2-3 is subtended by a scale arising from the midrib. The latter is nearly triangular in outline (Fig. 15*b*); having shortly lacinate margin in *P. ambigua*; nearly roundish-ovate and shortly lacinate in *P. Lyellii* and more or less similar in *P. longispina*.

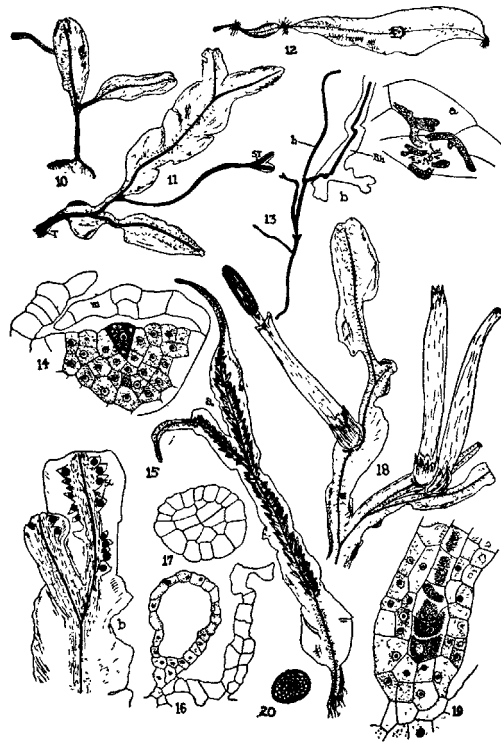
The antheridium is shortly stalked, nearly globular, with a single layered wall (Fig. 16), green when young and becoming orange at maturity. It resembles in its development the other Anacrogynous Jungermanniales. The initial makes its appearance as a papilla which soon enlarges and undergoes a transverse division to form an upper primary antheridial cell and a larger stalk cell. The latter enlarges and undergoes a transverse division to form a stalk, 2 cells long. Subsequently one or more transverse walls appear forming a stalk 3-4 cells long. Occasionally the original basal cell may undergo a vertical division before any transverse walls appear. It, however, remains short and is never more than 4 cells thick. The primary antheridial cell divides by a nearly vertical wall into 2 nearly equal halves. In each of the 2 primary antheridial cells 2 periclinal walls at right angles to each other are laid down, resulting in the formation of 4 peripheral cells and 2 primary spermatogenous cells. The latter divides by a transverse wall followed by a vertical one, appearing first in the lower half, or 2 vertical walls laid one above the other; dividing each spermatogenous cell into 4 quadrants (Fig. 17). The latter after regular vertical and transverse divisions form numerous spermatocytes, 4-5 sided in outline, densely laden with cytoplasm and each dividing diagonally to form 2 biciliated spermatozooids. The antheridial wall is one layered, chlorophyllous when young, becoming orange at maturity and breaking irregularly at the apex during dehiscence. The spermatozooids are liberated in a mucilaginous mass, are coiled, with 2 long cilia at the anterior end and a small vesicle at the posterior end.

FEMALE PLANT

They are as large or larger than the vegetative plants. Archegonia develop in groups in restricted areas, female inflorescences (Frye and Clark, 1937) or receptacles (Smith, 1938) at various points on the dorsal surface of the thallus along the midrib (Fig. 18). They are formed near the apex of a shoot but do not check its growth. Each is about the midrib in diameter and there is no correlation between their position and dichotomy of the thallus as in *P. zollingeri* (Campbell, 1939) but they might occur at each branch of the dichotomy; usually solitary at a point but

in *P. Lyellii* occasionally met with in a series. Around the receptacle grows a sheath, the involucre, from the surface of the thallus. It is short, cupulate, irregularly lobed; mediumly 1-2 lacinate in *P. ambigua*, unequally lacinate with each lacina comparatively thinner, forked and more branched in *P. Lyellii* and broadly lacinate in *P. longispina*.

During the development of archegonium a papilla-like cell makes its appearance from the receptacle surface and soon undergoes a transverse division usually to form a larger, rarely smaller or nearly equal, basal cell and an upper archegonial initial. The latter is cut off by 3 intersecting vertical walls into an axial cell and 3 peripheral cells. The axial cell divides by a transverse wall into an upper cover cell and a central cell. The latter undergoes another transverse division cutting off nearly equal cells, the upper neck canal cell and the lower ventral cell; but the divisions in the two cells are not simultaneous. Later divisions are similar to those



FIGS. 10-20.

- Fig. 10. *P. longispina* showing erect habit. $\times 2\frac{1}{2}$.
 „ 11. Same showing a stolon (ST) and a tuber of the previous season (T). $\times 2\frac{1}{2}$.
 „ 12. Same with walking habit. $\times 5$.
 „ 13a. Mycorrhiza (inter- and intra-cellular) in ventral tissue of thallus. $\times 212\frac{1}{2}$.
 „ 13b. Same, branched and entering a rhizoid (h hypha, Rh rhizoid). $\times 100$.
 „ 14. Apical cell in L.S. (m mucilage hair). $\times 162\frac{1}{2}$.
 „ 15a. *P. ambigua* (male plant). $\times 2$.
 „ 15b. Same, apical region only shown (a, antheridium; sc, scale). $\times 5$.
 „ 16. *P. ambigua*, mature antheridium and a scale in L.S. $\times 16$.
 „ 17. Same, T.S. young antheridium. $\times 162\frac{1}{2}$.
 „ 18. Female plant of *P. ambigua*. $\times 2\frac{1}{2}$.
 „ 19. V.S. archegonium (basal portion only shown), *P. ambigua* showing two ventral canal cells and two eggs within the venter. $\times 162\frac{1}{2}$.
 „ 20. Spore of *P. Lyellii*. $\times 162\frac{1}{2}$.

described for other Jungermanniales (Campbell, 1939; Finlayson, 1950; Mehra and Vasisht, 1950; Mehra and Khanna, 1950). The neck is elongated and more or less twisted in the mature archegonium. The number of neck cells varies from 5-11, with 8-23 cells in each row of the neck. The neck canal cells in the mature archegonium are 9-13 in contrast to 5-6 in *P. radiculosa* (Campbell, 1939). The ventral canal cell is angular, spherical or disc-shaped, and usually smaller than the egg or rarely more or less equal in size. Rarely 2 ventral canal cells and eggs are observed within a venter in *P. ambigua* (Fig. 19). Two eggs also occur in *Petalophyllum indicum* (Mehra and Vasisht, 1950) where one of the ventral canal cells behaves as the second egg. The venter becomes 2-3 layered after fertilization. The basal cell of the archegonium forms 2-6 cell long stalk after undergoing transverse and vertical divisions.

The involucre develops from the surface of the thallus around the group of archegonia in the form of a ring of scales which become united due to basal zonal growth and remain free at the apex, where each is lacinate. When mature it is 2-3 cells thick at the base and one cell at the apex.

The development of the perianth is stimulated if a single or more archegonia are fertilized. It grows next to involucre, is 3-4 cells thick at the base, cells in mature condition are thick walled, 4-6 sided, elongated and long. Sometimes it forms inside 1-4 knobs projecting inwards and up to 3 cells broad. At maturity it is tubular and covers the young sporogonium completely.

Just before fertilization the neck canal cells and the ventral canal cell become mucilaginous and presence of moisture brings about their distension which forces apart the 4 lid cells, each of which usually bends outwards to create a cup-like depression or occasionally the force of distension is so great that it forces the lid cells to break off from the neck. The spermatozoids enter in a mass but ultimately one fertilizes the egg.

SPOROGENIUM

A single sporogonium develops per receptacle due to nutritional competition, though more than one or all archegonia may be fertilized. The fertilized egg becomes nearly spherical in outline, enlarges, delimits its own wall and completely fills the venter. It forms a 3 celled filamentous embryo which is later differentiated into a foot, seta and a capsule. The foot is distinctly demarcated from the seta unlike in *P. radiculosa* (Campbell, 1939) where it merges imperceptibly into the base of the seta. It is about 1 mm. long in the young sporogonium, composed of parenchymatous cells with dense protoplasmic contents in the peripheral cells which are haustorial in nature. The seta is circular in outline, in a cross-section composed of 9 cells, made up of numerous elongated cell rows; cells thin walled, usually chlorophyllous and in the younger stages filled with starch grains. In a L.S. the cells are much compressed, broader than long but in the mature condition they elongate and attain a length several times their original. The seta is slender, whitish, 5-7 cm. long in *P. ambigua*, 3.4-5 cm. in *P. Lyellii* and *P. longispina*. Rarely its peripheral region develops a few false air spaces by disintegration of the adjoining cell walls; they bulge outwards and open to the exterior by their entire surface. The seta provides a good substratum for the growing sporelings dehiscid from the capsule and for filamentous algae.

The capsule is oblong cylindrical, green when young, reddish-brown at maturity, 5 mm. long, 0.5-1 mm. in diameter, with 2-3 layered wall—the inner getting resolved and the outer becoming dark brown with development of thickenings towards their inner angles. The elaters are attenuated, thin walled, with 2-3 spirals; up to $600 \times 6\mu$ in *P. ambigua* and $200 \times 5\mu$ in the other two species. Some of them remain attached to the base of the capsule. Spores are spherical, light-reddish brown, with an indistinct triradiate mark and finely reticulate exine

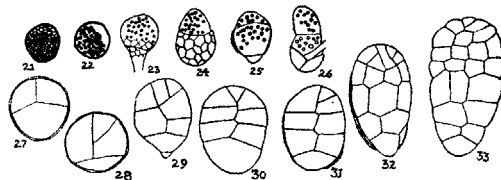
(Fig. 20); 12–16 μ in *P. ambigua*, 12–28 μ in *L. Lyellii* (with margin papillate) and about 12 μ in *P. longispina*.

The calyptra ensheathing the young capsule is thin, slender, 2 cells thick, with the cells much longer than broad.

When mature the capsule is gradually pushed up due to the elongation of the seta and pierces through the calyptra finally coming above the surface of the thallus. It dehisces along (2), 3, (4) valves at maturity, the latter remaining coherent at the apex. Their splitting starts at the base of the capsule and just reaches the apex where all the cells are highly thickened. This prevents their complete separation.

SPORE GERMINATION

The spores of *P. ambigua* and *P. Lyellii* germinate while still within the capsule as in *Pellia*, *Porella* and *Conocephalum* (Chalaud, 1932) and *Dumortiera* (unpublished data). Wolcott (1942) does not describe intracapsular germination in *P. Lyellii* collected from Texas. (Germination is not studied in *P. longispina*). Each spore enlarges slightly or greatly as evidenced by distension of reticulations (Fig. 21); the chloroplasts aggregating to one side (Fig. 22)—probably towards the side facing capsule wall; leaving a small clear space towards the opposite end as in *Pellia* (Goebel, 1905). The latter is cut off by a wall and forms the first rhizoid (Fig. 23). The enlargement of spore results in an irregular rupture of exine, either to liberate the germ papilla (Fig. 24) or the rhizoid (Fig. 25) or the cell mass develops inside (Fig. 30). Occasionally the exine ruptures along the indistinct triradiate mark and the germ papilla elongates into a germ tube (Fig. 26). The upper half of the germ cell now undergoes a vertical division (Fig. 27) and later a wall is formed inclined obliquely to the long axis of the germ cell to form an apical cell with two cutting faces (Fig. 28) as in *Metzgeria* (Goebel, 1905) and *Riccardia indica* (Kachroo, 1953), or the upper cell may undergo a few transverse divisions before a vertical wall appears and an apical cell is formed due to formation of two walls oblique to each other. Activity of this cell results in an enlarged cell mass (Figs. 29–33) and it is gradually lodged within an apical notch, where mucilage papillae are formed from the surrounding marginal cells of the thallus to protect the growing region.



FIGS. 21–33. Stages in germination of spores up to formation of cell mass in *P. ambigua* and *P. Lyellii*. Figs. 21–25, 27 and 28 intracapsular and rest from soil culture. $\times 200$.

Variations in certain characters of the thallus, organs associated with sex organs and their bearing on species problem in the genus :

Thallus : The great deal of variation in the species embraces their vegetative growth, both while growing under different habitats (Table I and Fig. 34), altitudes (Tables 2 and 3) and within the same community (Figs. 35–37). It appears that substrate exerts considerable influence on the growth (Fig. 34). Thus large numbers of conducting cells occur in the epiphytic forms due to conservation of water and this might also speak for less breadth of the thallus to check excessive transpiration; in those living on humus the need for conservation is far less, consequently this region occupies a comparatively smaller area of the midrib and the largest breadth of the thallus (in this case) might be due to prolific vegetative growth under congenial conditions of life. The next congenial habitat is shady soil.

TABLE 1

*Variation in vegetative growth of P. Lyellii under different habitats**

Habitat	Thallus breadth	Thallus thickness		Epidermal cells		Area C.S. in T.S.	Number of cells in T.S.	
		Midrib	Wing	Marginal	Middle		Midrib	C.S.
	mm.	μ	μ	μ	μ	μ		
A. On rotten wood	3-3.2	214.4	48	32 × 89 μ	64 × 64 68 × 50	64 × 54	33	12
B. Epiphytic	2.5-5.1	304	48	28.8 × 57.6	46 × 46 28.8 × 41.6	64 × 76	45-90	12
C. On soil rich in humus	6	320	54.4	22.4 × 70.4 57.5 × 89	57.6 × 89	48 × 60.8	36	12
D. Shady banks	4	384	48	22.4 × 73.6	44.8 × 64	64 × 105	60	15
E. Moist hill slopes	4	304	46	27.2 × 57.6	41.6 × 32	51 × 64	24	13

* Plants with 1 or more female receptacles are regarded here as well developed thalli. Each reading given is an average for 5 thalli.

The readings of thickness of thalli, epidermal cells and conducting region have been taken at corresponding places in the thalli of various groups.

C.S.—Conducting strand, midrib does not include conducting strand (same details for other tables). T.S.—Transverse section.

The growth of *P. Lyellii* and *P. longispina* under different altitudes (Tables 2 and 3) shows that the species are not fundamentally affected as far as their vegetative features are concerned and the latter, therefore, do not show any correlation with the change of altitude. The variations exhibited are those which are expected even while they grow in a single community. However, this requires further study and a care in collection of the various forms at different altitudes.

TABLE 2

Variation in vegetative growth of P. Lyellii under different altitudes in Japan (Province, Hyuga—collection, Hattori, Jan.—Nov. 1950)

Altitude	Thallus breadth	Thallus thickness		Epidermal cells		Area C.S. in T.S.	Number of cells	
		Midrib	Wing	Marginal	Middle		Midrib	C.S.
m.	mm.	μ	μ	μ	μ	μ		
15	5	99	11.25 39 × 33	108 × 24	105 × 45	15 × 15	14	46
30	3	75	11.4	39 × 33 93 × 27 57 × 30	75 × 39 90 × 48 63 × 54	30 × 18	15	55
150	6.1	51	11.4	84 × 24 45 × 21	57 × 24 30 × 51	15 × 18	14	28
250	5.2	63	12	75 × 18 42 × 21	75 × 33 54 × 33	15 × 20	11	22

TABLE 3

Variation in vegetative growth of *P. longispina* growing on moist rocks under various altitudes in Japan (collection, Hattori, 1950)

Altitude	Thallus breadth	Thallus thickness		Epidermal cells		Area C.S. in T.S.	Number of cells	
		Midrib	Wing	Marginal	Middle		Midrib	C.S.
m.	mm.	μ	μ	μ	μ	μ		
5	2	176	36.8	54.4 × 19.2	28.8 × 35.2	48 × 32	12	36
20	2.5-3.5	320 (480)	38.4	80 × 28.8	35.2 × 48	76 × 106	20	74
400	4	288	38.4	70.4 × 22.4	64 × 44.8	38 × 80	15	63
700	4-6	256	38.4	48 × 22.4	38.4 × 86.4	48 × 73	15	56
800	4-4.5	256	40	80 × 19.8	74.6 × 38.4	48 × 35.2	16	36

The study of the species within a community (Figs. 35-37) illustrates that no two features usually show a correlation between them and that variability appears to be an inherent feature for each individual of the various species. (It is probable that microclimate has a dominating hand in shaping the individual). The epidermal cells, whether marginal or those towards the middle, are highly variable (Table 4) in size; so are the cells in the midrib and the area of the conducting strand.

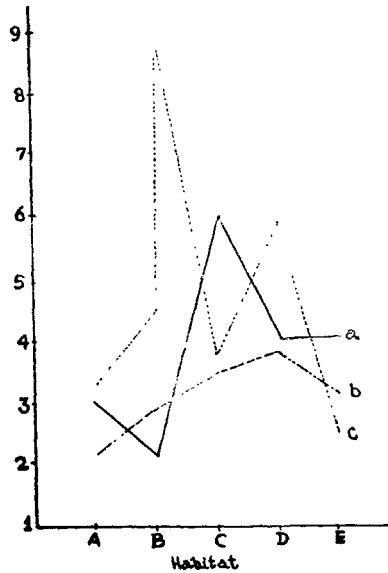
TABLE 4

Variability in epidermal cells of thallus

Plants	<i>P. ambigua</i>		<i>P. Lyellii</i>		<i>P. longispina</i>	
	Marginal	Middle	Marginal	Middle	Marginal	Middle
	μ	μ	μ	μ	μ	μ
1	48.4 × 28.5	54.1 × 28.5	51.3 × 31.3	100.9 × 39.9	39 × 30	57 × 39
	65.5 × 25.6	71.2 × 25.6	72.2 × 19.9	57 × 42.7	66 × 27	96 × 30
2	45.6 × 18.5	51.3 × 34.2	39.9 × 18.5	76.4 × 25.6	54 × 24	48 × 39
	57 × 25.6	76.4 × 25.6	27 × 25.6	28.5 × 51.3	60 × 21	66 × 33
3	51.3 × 31.3	57 × 18.5	42.7 × 31.3	51.3 × 39.9	45 × 24	57 × 42
	42.7 × 22.8	65.5 × 31.3	79.8 × 28.5	85.5 × 28.5	63 × 24	75 × 33
4	42.7 × 28.5	57 × 25.6	22.8 × 51.8	71.2 × 51.3	30 × 33	57 × 33
	65.5 × 17.1	74.1 × 28.5	28.5 × 57	65.5 × 34.2	63 × 18	75 × 30
5	57 × 25.6	79.8 × 22.8	42.7 × 37	48.4 × 48.4	42 × 33	45 × 24
	39.9 × 28.5	59.8 × 34.2	85.5 × 34.2	71.2 × 28.5	60 × 27	60 × 33

Antheridial scale: Usually a single scale ensheaths a single antheridium and such scales may have either one or more papillate protrusions towards the apex, or these may be prolonged into lacinae (teeth), or have neither; or the scale may be bifid or asymmetrical in outline (see Figs. 38 and 39 for the most common forms of the scales). Scales showing more than one lacina usually ensheath more than one antheridium within and in the case of scales holding their individuality (i.e. not fusing with adjoining ones) there appears to be a correlation between the number of lacinae and the number of antheridia ensheathed within—usually one antheridium per lacina, in *sensu lato*. In case of scales forming flaps this arrangement becomes obscure and it is noteworthy that in such cases usually antheridia do not

occur within the regions where adjoining scales fuse. It is not, however, uncommon to find antheridia unprotected (Fig. 38c), single lacinate scales with more than one antheridium, or many papillate-lacinate scales with a single antheridium or sterile scales. The formation of flaps is due to fusion of the bases of adjoining scales—the apical region being free and marking the number of the constituent scales distinct. Rarely scales are bivalved and appear as cups (Fig. 38o) with one or more antheridium within.



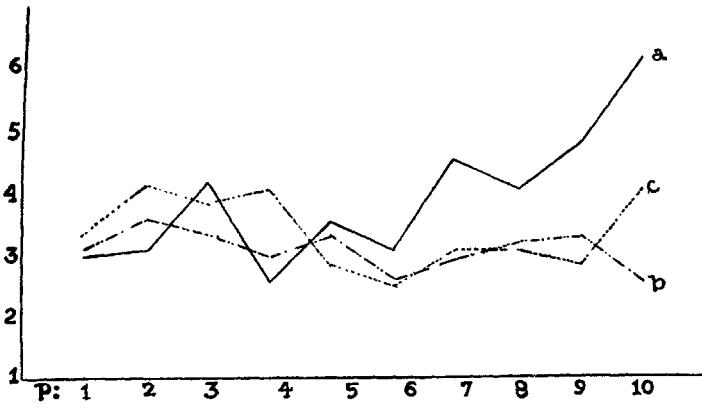
34

FIG. 34. Growth of *P. Lyellii* under different altitudes (a, thallus breadth; b, thickness of midrib; c, number of cells in midrib. A-E as in Table 1).

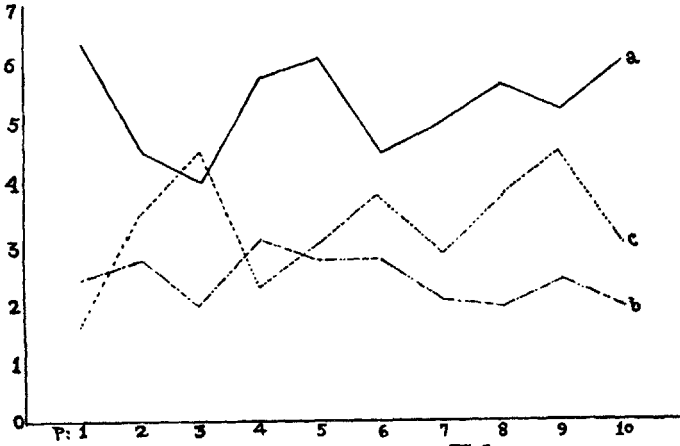
Involucre: Each species shows a great deal of variation in structure of involucre so far as the lacinae are concerned. Thus in *P. Lyellii* the primary lacinae are either thick, short, unbranched or branched, 1-2 times at the base; in form of plates or they are thin, longer, less branched or more branched; the tips becoming glandular (Fig. 40, a-c). Similar variations occur in the other species but there the lacinae are less branched and more or less plate-like, being thus clearly distinguishable from the above type (Figs. 41 and 42).

Perianth: The mouth of the perianth is variable both in opening and in the incidence of lacinae. The mouth may be cut into a few fid or partite lobes, each shortly or broadly lacinate; or the partitions may be deeper or it may be cut into 4 lobes forming a beak-like structure. A few variants are figured for *P. Lyellii* (Fig. 43). Whereas usually the developing sporogonium emerges through the apex of the perianth, lateral emergence is not uncommon (Fig. 43, h).

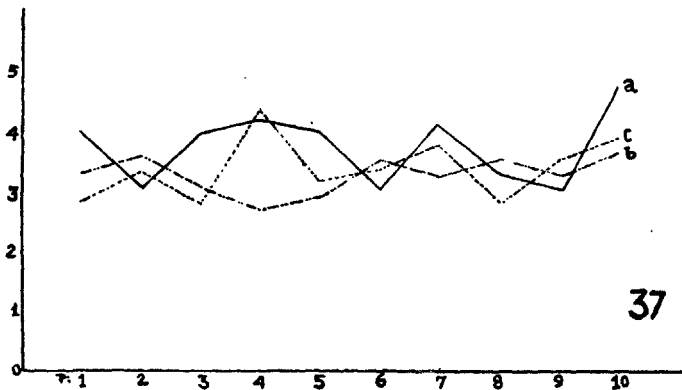
These variations bring forth interesting results involving specific characters and note should be taken of the same while dealing with imperfectly known species (cf. *P. canarus* (vide Pande and Srivastava, 1954) might on this basis be simply a biologic form of *P. Lyellii*) or while describing new species. Cytological investigations might throw more light on this problem.



35



36



37

Figs. 35-37. Variation in growth of *P. ambigua*, *P. Lyellii* and *P. longispina* respectively growing on moist soil (legend as in Fig. 34); P, plants.



FIG. 38a-q. Variations in antheridial scale in *P. ambigua*. $\times 22\frac{1}{2}$.

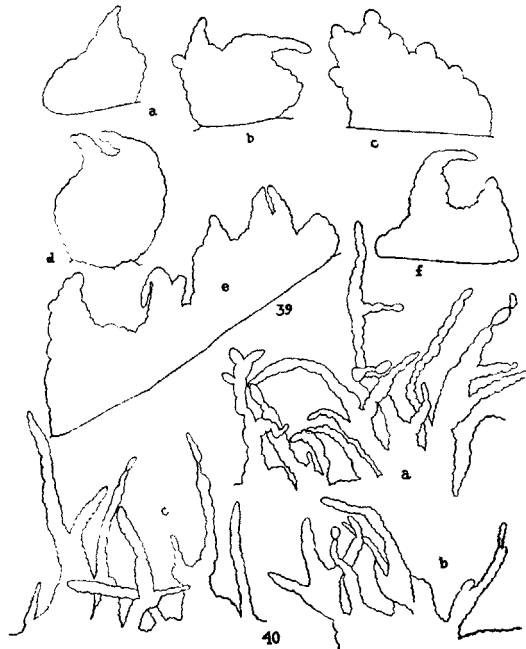


FIG. 39a-f. Variations in antheridial scale in *P. Lyellii*. $\times 22\frac{1}{2}$.

„ 40a-c. Showing variations of lacinae in different involucre of *P. Lyellii* (only a portion shown). $\times 22\frac{1}{2}$.



FIGS. 41-42. Fig. 41a-d. Showing variations of lacinae in different involucre of *P. ambigua* (a portion shown). $\times 22\frac{1}{2}$.
Fig. 42a-b. Same on *P. longispina*. $\times 22\frac{1}{2}$.

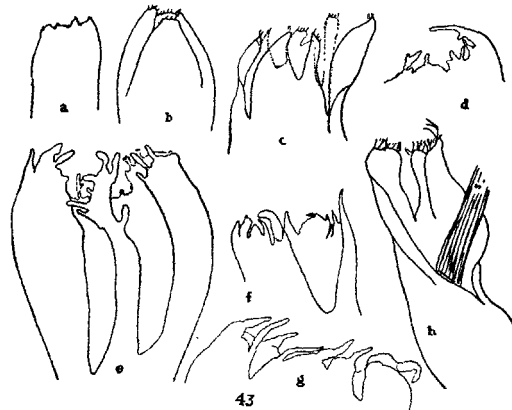


FIG. 43a-g. Showing variations in mouth of perianth and nature of lacinae in *P. Lyellii*; h lateral emergence of sporogonium. a-f $\times 10$; h $\times 22\frac{1}{2}$.

Thus the epidermal cells are not reliable as specific characters, nor are the antheridial scales. But the nature of the involucre, particularly its lacinae (though variable), might be considered reliable for the species to be classified into two groups: those with profuse branched, thin, elongated lacinae (*P. Lyellii* type) and those with less profuse branches and thick plate-like lacinae (*P. ambigua-longispina* type); this goes, to some extent, hand in hand with the presence of the marginal teeth on the thallus, at least in the present case. The mature capsule is too uniform and the

perianth quite variable; the spores also do not show marked inter-specific variation. It is probable that a comparative study of all the 40 species of the genus, on the lines suggested here, might reveal large variation among the species and a number of the latter might turn up to be simply the various biologic forms of but a few species.

Individuality of the family Pallaviciniaceae :

Cavers (1911) in his arrangement of genera under Blyttiaceae places *Pallavicinia* before (i.e. primitive than) *Symphyogyna* and family as number 3 in his division of Anacrogynae. Goebel (1930), followed by Campbell (1939), regards the group as sub-family: Pallaviciniaceae, and places it as ii order in his division of Metzgeriaceae. He placed *Pallavicinia* and *Symphyogyna* only in his sub-family. But like Cavers he recognizes the difficulty of clearly defining these families (Campbell, 1939, p. 121). Verdoorn (1932) includes the genus in his Dilaenaceae which also embraces Goebel's Pallaviciniaceae and Morckiaceae. Frye and Clark (1937) recognize *Pallavicinia* as most primitive member in their Metzgeriaceae and derive it from *Geothallus* through some intermediate form (*F* in their phylogenetic table on p. 104). Smith (1938) regards it as a form between two extreme types: *Riccardia* and *Fossombronia* respectively and remarks 'genera placed in Riccardiaceae have no one feature common distinguishing them from other Anacrogynae (p. 49)'.

In species of *Pallavicinia* studied here, it is usual to have a basal rhizomatous and an ascending photosynthetic region, but it is noted that thalli grown separately under optimum conditions do not form rhizomatous region. Suppression of wings is common and is either on the side facing substratum or on both sides as in *Umbraculum* (Goebel, 1905). The nature and formation of lobes in the thalli is similar to that exhibited by *Symphyogyna*, *Fossombronia* and a few other genera of Anacrogynae. Such developments may have taken place independently in the various families and does not necessarily prelude any near relationships. There is not enough evidence to show that such lobes are leaves, though their presence suggests leafy ancestry.

An inner central conducting strand is also present in *Symphyogyna* (Finlayson, 1950), *Umbraculum*, *Podomitrium* and some species of *Riccardia* and *Metzgeria* (Goebel, 1905). In having an apical cell with two cutting faces the genus resembles *Symphyogyna*, *Riccardia*, *Metzgeria*, *Umbraculum*, *Fossombronia himalayensis* (Pande *et al.*, 1953) and *Calycularia crispula* (Pande and Udar, 1953) but differs from *Petalophyllum indicum* (Mehra and Vasisht, 1950) and *Sewardiella tuberifera* (Mehra and Khanna, 1950) which have tetrahedral apical cell. The intra- and inter-cellular mycorrhiza is a feature common to all the thallose Jungermanniales. Tubers also occur in the related family Codoniaceae, probably due to similar biological adaptations.

The presence of a cup-like involucre is an advance over the single one of *Symphyogyna*, which Goebel (1930) regards as the original one. In *Umbraculum* and *Metzgeria* an involucre is present or absent. In Codoniaceae the involucre bracts are scattered irregularly among the archeogonia and are attached at the base. A tubular perianth is also present in *Podomitrium*, *Calycularia* and *Petalophyllum* (Campbell, 1939; Goebel, 1905) but it is absent in *Symphyogyna* and *Metzgeria* (Goebel, 1930). *Riccardia* is peculiar in having neither, and in developing a massive marsupium quite different in origin from calyptra of *Pallavicinia*, this together with the development of an elaterophore is a specialized feature.

The structure and development of sex organs and sporogonium resemble more closely that in *Symphyogyna* (Campbell, 1939; Finlayson, 1950) than with any other genus. The capsule wall is two layered as in *Fossombronia* and unlike that in *Riccardia* and *Calycularia* where it is three layered. A few elaters might remain attached to the base of the capsule. The embryo is filamentous as in *Symphyogyna*

and *Riccardia*. The dehiscence of capsule is along 2-4 valves which remain attached at the apex as in *Symphyogyna* and in contrast to *Riccardia* where they separate and carry a portion of elaterophore at the apex. The germination of spores shows great similarity with that of *Symphyogyna* and *Pellia*.

Pallavicinia, thus, shares many features with primitive and advanced genera of Anacrogynae, yet retaining its individuality and distinctness from the genera with which it is kept by Verdoorn (1932), Frye and Clark (1937) and Evans (1939). Goebel (1930) and Campbell (1939) are justified in placing it with *Symphyogyna* in a separate family Pallaviciniaceae. With most of the genera it follows parallel lines of development in habit and divergent features in life-history; thus taking view of the contemporary morphology of Hepaticae the various genera or groups of genera should be regarded as end products of long and diversified evolution. This necessitates and justifies the division of Anacrogynae into various families. Each group has further developed special individual features. The intimate relationship between them, however, speaks for a common group of ancestors.

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ABSTRACT

Pallavicinia ambigua, *P. Lyellii* and *P. longispina* occur in patches, usually in moist places. Each has a basal rhizomatous region and an ascending assimilatory region. A mid-dorsal vein and an inner central conducting strand is present. It is connected with that of forking but not with that of adventitious branch. An apical cell with 2 cutting faces is present in the sporangia and the thallus, it cuts segments alternately right and left. Development of sex organs resembles other Anacrogynae. Two eggs and 2 ventral canal cells are observed in an archegonium. The embryo is filamentous. Rarely air spaces develop on the seta. Capsule is oblong-cylindrical and dehisces along 2-4 valves, attached at the apex. Spores germinate while still within the capsule, form a cell mass with 2 sided apical cell. A detailed study of the variations in certain characters of the thallus, organs associated with sex organs, is given and the specific value of the various organs discussed. It appears the species problem leans heavily on the nature of the lacinae on involucre and marginal teeth of the thallus. The retention of the family Pallaviciniaceae with *Pallavicinia* and *Symphyogyna* is suggested.

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