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ON THE MORPHOLOGY OF THE GAMETOPHYTIC GENERATION OF *PADINA GYMNOSPORA* (KUETZ.) VICKERS

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INTRODUCTION

THE genus *Padina* has about a score of species of which *P. gymnospora* (Kuetz.) Vickers alone is known to have a discontinuous distribution, occurring on the one hand in the West Indies, and on the other in Mauritius and India (Kuetzing, 1859 ; Vickers, 1905, 1908 ; Boergesen, 1914, '30, '37, '41, '48 ; Taylor, 1942, '43). In both the regions the gametophytes of this species appear to be rare. Two oogonial specimens which were in the Berlin Botanical Museum were studied by Kniep (1928, pp. 178-85), but details were not given about their morphology and place of origin. The writer collected four oogonial and two antheridial plants 12.8 km. west of Mandapam, at Puthumadam in the Gulf of Manaar, where they were obtained from shore-seine fishing nets which contained large numbers of tetrasporic plants as well. An oogonial plant and a few tetrasporic plants were dredged from a depth of 5.5 m. at 1.5 km. east of the place and 90 m. off-shore. An oogonial plant was found growing with numerous tetrasporic plants of the species, on Galaxea Reef (Krusadi I.), at a depth of 0.6 m. during low tide and another was found cast up at Pamban ; four oogonial plants were collected from a depth of 1.2 m. at low tide from Mandapam Camp (Palk Bay).

The antheridial plant, collected on 6th January, '53 which was the 6th day after full moon (*vide* Swamikannu, 1923), showed antheridia with sperm mother-cells at the early stage. The antheridial plant obtained on 29th January, '53 which was, full moon day showed mature sperm mother-cells. The three oogonial plants collected on the 5th and 6th (2 plants) days after new moon and the two oogonial plants collected on the 7th and 9th days after full moon showed immature oogonia. The oogonial plant collected on full moon day and the four collected on the 1st day after full moon showed mature oogonia. That the oogonia and the antheridia mature simultaneously at full moon and new moon is probable from the present specimens. In the allied genus *Dictyota*, Williams (1904 b, p. 183) found that the oogonia and antheridia are produced in fortnightly crops which begin to develop at the lowest neap tide and mature at the following highest spring tide, the gametes being liberated in the next few days.

The male gametophyte of *P. gymnospora* (Kuetz.) Vick. has not been reported before, and the two examples in the present sequence as also a male plant from Mombasa, Kenya, found in the Herbarium of the New York Botanical Garden, bearing the legend ' *ex* herb. Hauck No. 38 ', which was determined by the writer, are therefore of interest. These collections definitely show that this species has a gametophytic generation with unisexual plants and that *P. australis* Hauck in which the gametophytic plant is bisexual (unpublished) is distinct from it though synonymised with it by Boergesen (1930).

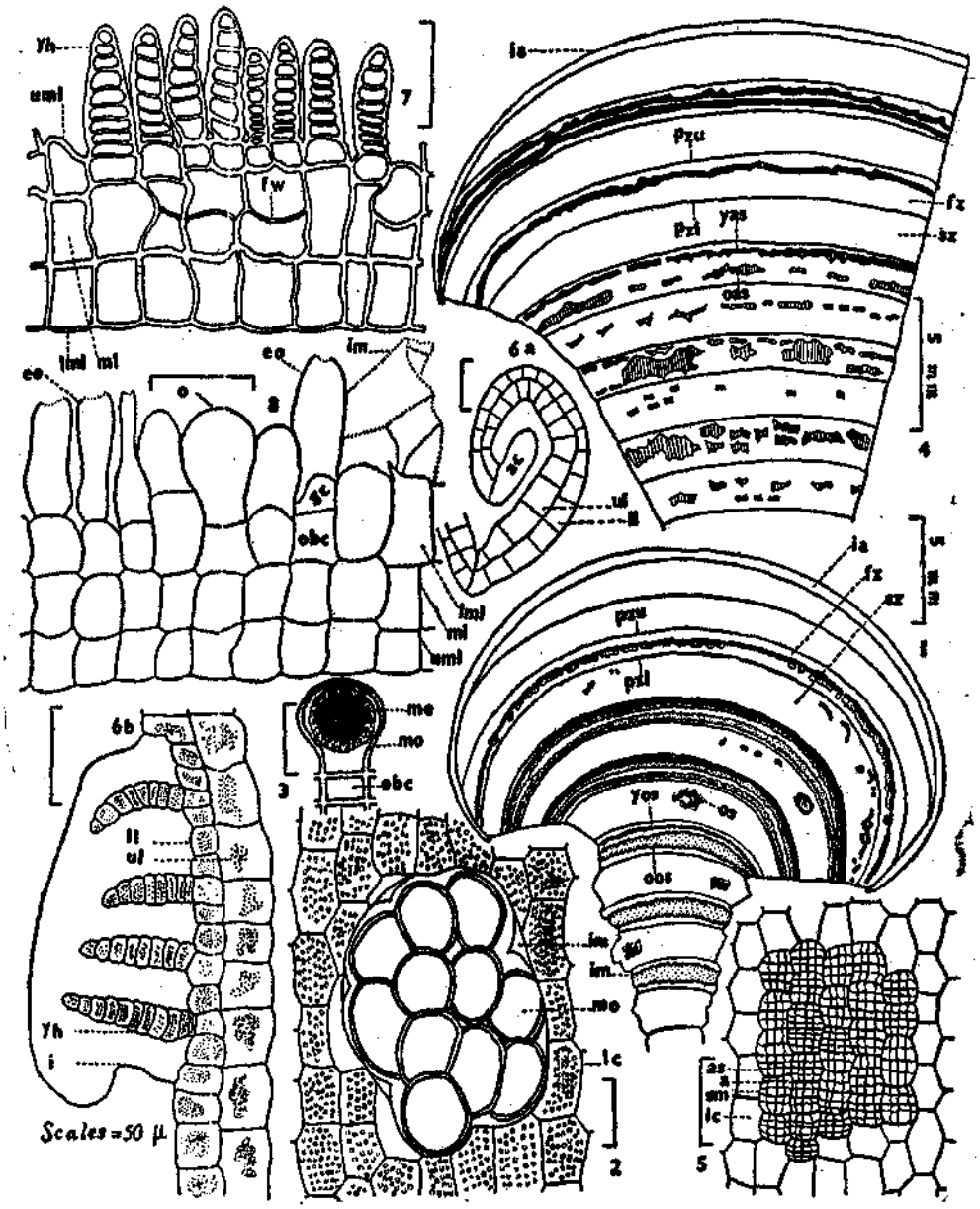
General Morphology

In the Mandapam area, the tetrasporic plants are usually larger than the oogonial and antheridial plants. All of them have the greater part of the frond made up of three layers of cells, *i.e.*, from about 1 to 2 cm. behind the involute apical border to the base of the frond, which is in general agreement with the description given by Boergesen (*l.c.*, p. 171) ; the involute part behind the row of apical cells, and the very young part of the spread-out region down to 1-2 cm. from the involute part have only two cell layers. The inferior part of the stipe of the plant in some individuals is formed by the complanate juvenile stage called *der Flachtrieb* by Reinke (1878, p. 16, pl. 3, Figs. 1-4), in which case the cross section of this region shows in one and the same section 6 layers in the median part and 3 or 4 layers at both ends of the section. Hauck (1887, p. 41) says the region of the stipe, in the genus, may be formed by the earlier terete juvenile stage (*der Rundtrieb*) in consequence of which the region would show more cell layers than the frond proper (*der Breittrieb*). In this species, as found here, the cells of the uppermost layer of the frond and those of the middle layer are on the average longer than those of the lowermost of the three layers.

The width of the fertile zones of the frond is slightly to distinctly less than that of the sterile zones, and the two types of zones alternate, which is as figured by Boergesen (1914, Fig. 30). However, sori often develop in the broader zones in addition to being present in the narrower zones. In the three phases of the species as growing in our area, the lower surface of the frond which unlike the upper is not coated with a film of lime bears the sori ; but in addition, a weaker development of sori on the upper surface may often be seen in the tetrasporangial and antheridial plants, though not commonly in the oogonial. The oogonial plant may be distinguished from the tetrasporangial chiefly by the sorus in the former being more compact and narrower than in the latter. The oogonial sori vary in width from 0.2 to 0.9 mm. and the tetrasporangial from 0.5 to 1.5 mm. Further the oogonial sorus is indusiate but not the tetrasporangial. The indusium of the oogonial sorus is the external layer of the outer walls of the oogonia which gets separated and raised up as the sorus matures, forming a thin dome over it. As the oogonia enlarge the indusium gets torn away and only its margin persists as a white cuticle around the fairly mature or empty sori as the case may be (Figs. 1, 2, 8, 10, 11). The diameter of the mature oogonia, 60-70 μ, is much less than that of mature tetrasporangia 90-125 μ. In the antheridial plant also the sori are compact and have about the same width as those of the oogonial plant, but an indusium over the antheridial sorus is rarely seen in the present material. Meiosis in the tetrasporangium has been shown to occur in *P. pavonia* (L.) Gaillon by Williams (1904 *a*), Georgevitch (1918 *a*) and Carter (1927).

Oogonial Plants

The oogonial plants vary from 4 to 11 cm., in height, from the holdfast to the apex, the expanse being rather more than the height. The basal part of the plant is stupose on both surfaces. Both the surfaces have alternately wider and slightly narrower zonation, the former being 1.5 to 3.0 mm. wide. The upper surface is thinly coated with lime. In the younger regions of the frond the broad zones tend to be sterile but the narrower are fertile (Fig. 1). In the older regions both the types of zones may be fertile, the sori developing later and to a less degree in the broad zones. The inferior line of the narrower zones is formed by a piliferous band



FIGS. 1-8. *Padina gymnospora* (Kuetz.) Vickers

1. Lower surface of oogonial plant. 2. Surface view of mature oogonial sorus. 3. Mature oogonium from sagittal section of frond. 4. Lower surface of antheridial plant. 5. Surface view of antheridial sorus. 6*a*. Sagittal section of apex of frond. 6*b*. Sagittal section showing piliferous band on the outside of the involute apex. 7. T. S. frond with piliferous band on upper surface. 8. T. S. frond showing oogonial stages.

a-antheridium. *ac*-apical cell. *as*-antheridial sorus. *eo*-empty oogonium. *fw*-frontal wall. *fz*-fertile zone. *i*-indusium. *ia*-involute apex. *im*-indusial margin. *lc*-lower-surface cell. *ll*-lower layer. *lml*-lowermost layer. *me*-mature egg. *ml*-middle layer. *mo*-mature oogonium. *o*-oogonium. *oas*-old antheridial sorus. *obc*-oogonial basal cell. *oos*-old oogonial sorus. *os*-oogonial sorus. *pzl*-piliferous zone on lower surface. *pzu*-piliferous zone on upper surface. *sc*-subsidiary cell. *sm*-sperm mother-cell. *sz*-sterile zone. *ul*-upper layer. *uml*-uppermost layer. *yas*-young antheridial sorus. *yos*-young oogonial sorus. *yh*-young hair.

on the lower surface of the frond, and the superior by one on the upper surface, and in the case of the broad zones it is the opposite. Boergesen (1930, p. 171) observed that in this species the piliferous bands are placed alternately on the upper and lower surfaces, but it has to be indicated that he had taken the upper surface to be the lower and *vice versa*, a confusion which appears to have arisen from Hauck's statement (*l.c.*) that chiefly the upper surface bears the sori, in the genus.

In the upwardly rolled margin, there is at the very edge a single layer of apical cells. Immediately behind them the frond is two layered and remains thus in the various turns of the rolled up part (Fig. 6*a*). At first the two cell layers are of equal depth, later the inner (upper) becomes deeper than the outer (lower). On the outer layer there are one or two piliferous bands (Fig. 6*b*), the hairs dropping off as the rolled up apex unfurls, but later new hairs are formed from the same initials. The piliferous bands of the upper surface arise anew some distance below the rolled up margin (Figs. 7 and 12*a*). Bitter (1899, p. 22) has proved that the hairs develop in reaction to strong light. When the rudimentary hairs grow out into long monosiphonous hairs, a peculiarity is noticed in the Mandapam plants, namely that new walls are laid down inside the old walls of the cells of the rudimentary hairs, and while the new walls of each segment elongate, its old walls remain at the base of the segment and are seen usually as two minute spikes, one at either end of each transverse septum or at times as a complete collar (Fig. 12*b*).

The depth of the cells of the upper layer, in the 2-layered region of the frond, below the involute apex, is 35.0-59.5 μ, of the lower layer 24.5-38.5 μ; the width of the cells of both the layers, 17.5-24.5 μ. The cells of the upper layer are longer on the average than those of the lower, their length varying between 28-84 μ (usually 35-70 μ) and between 17.5-59.5 μ (usually 28-42 μ) respectively. From about 1-2 cm. below the involute apex to the basal part, excluding juvenile stages that may be present at the base, there are 3 cell layers ; this increase to three layers results from the periclinal (frontal) division of the upper of the original two layers (Figs. 7 and 11). In the middle part of the frond the depth of the two upper layers is about 26.3 μ each, of the lowermost layer, generally 35.0 μ, but in the basal part all three layers are usually equal in depth, each layer being about 35.0 μ in depth. Both in the middle and basal parts of the frond the width of the cells of all three layers is equal, varying from 21-28 μ, the cells appearing in tiers in transverse sections of the frond (Figs. 7 to 9 and 13). The length-range of the cells of the two upper layers is greater than that of those of the lowermost layer (Fig. 10), the former 35-70 μ, the latter 17.5-42.0 μ with the majority being 35.0 μ long in the case of the lowermost layer.

The oogonial sori are borne almost exclusively on the lower surface in our specimens, and the young sorus is a continuous or an interrupted band, 120-422 μ wide, with jagged margins. There may be one to three bands of sori in a zone which are formed successively towards the apical margin (Fig. 1), or a young band is seen on either side of an old band. The oogonial mother-cells develop from superficial cells by increase in height (Fig. 9), and when it is between 49 and 52 μ a cell is cut off at the base of each mother-cell, the upper cell developing into the oogonium (Fig. 10). The mature oogonium is like an inverted sphaerical flask about 60 to 70 μ in diameter, the neck being very short (Fig. 3). The basal cell of the oogonium is in length, 25-35 μ, in height and width, 21-28 μ. The indusium becomes visible, in surface view and sections of the frond, when the sori are fairly

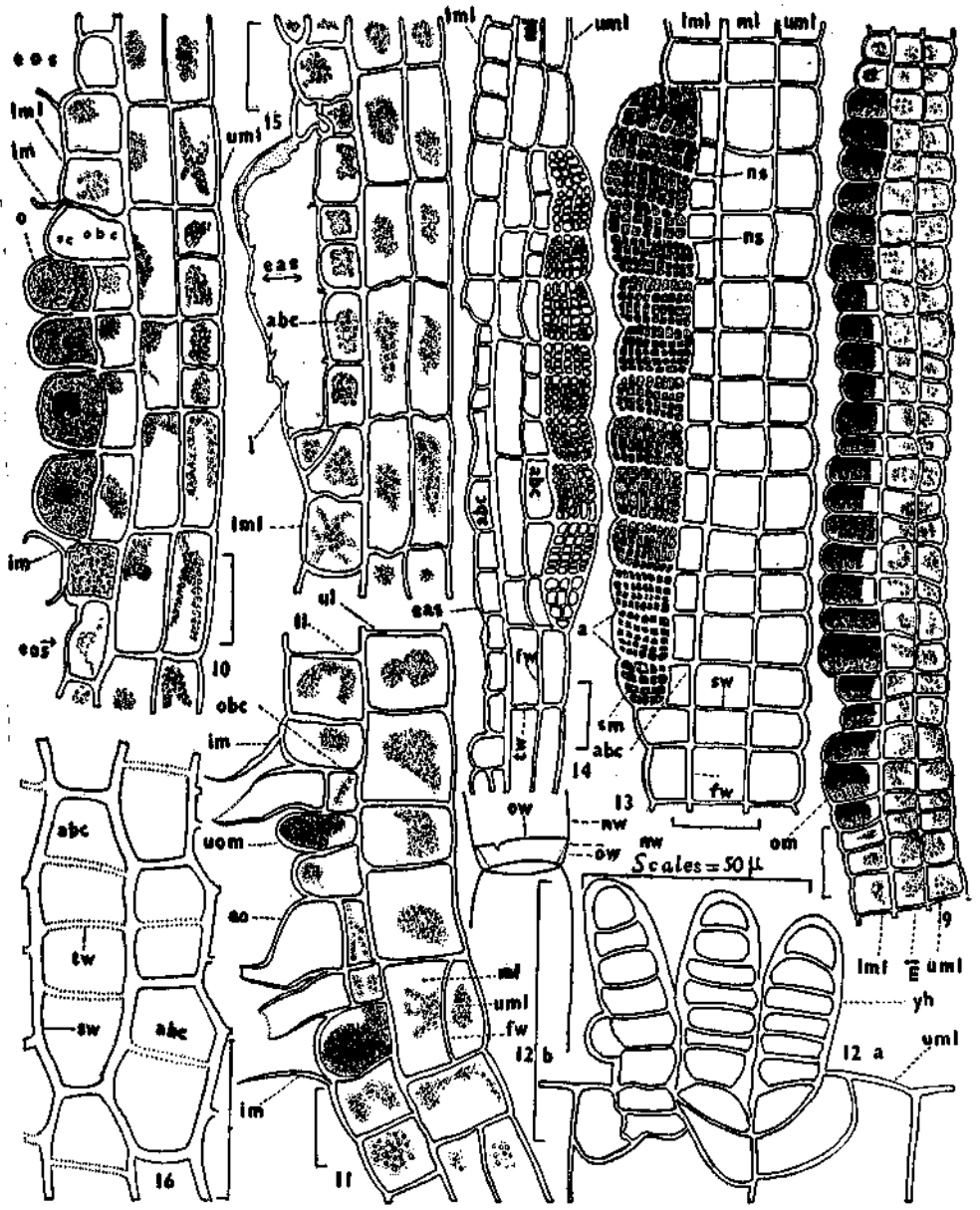
mature (Figs. 2, 10, 11). After liberation of the eggs the empty oogonia are seen, in sections of the frond, as vertical, sub-cylindrical cells, open at the top, 52-70 μ by about 35 μ, and densely arranged, with at times a few intervening cells (Fig. 11, *uom*). The basal cell, in rare instances (Figs. 8 and 10), divides, cutting off a cell towards the periphery which is known as the subsidiary cell. Such divisions of the basal cells have been described as occurring in *P. pavonia* (L.) Gaillon, the upper halves developing into secondary oogonia (Reinke, *l.c.*, Georgevitch, 1918, *b*).

Whereas fertilization and germination in the genus normally occur after the eggs are shed, germination *in situ* was seen in some of the present plants. Wolfe (1918, pp. 88-89) found in *P. vickersiae* Hoyt that the eggs may at times be fertilized before they are shed. He also found that eggs which remained unfertilized after having been shed occasionally showed parthenogenetic development but failed to grow into mature plants. Vegetative reproduction by propagula that develop terminally or laterally on mature hairs of the piliferous zones of the frond was noticed in one of the present oogonial plants. Küster (1899, p. 159) describes propagula arising on rhizoid-like filaments growing on the lower surface of the frond in *P. pavonia* (L.) Gaillon.

Antheridial Plant

The antheridial plant (C.M.F.R.S. Herbarium No. 1013) is 14 cm. in height from the holdfast to the apex, and 16 cm. in expanse. It is deeply divided into cuneate lobes and is to a good extent incrusted by a *Corallinaceae*. The wider zones on the two surfaces of the frond are 1.5 to 2.5 mm., and they alternate with slightly narrower zones (Fig. 4). The lower surface has far more extensive sori than the upper. On the lower surface, in some of the younger parts, there is an alternation of fertile narrow, and sterile broad zones; but for the most part, adjoining zones of both types are fertile. On the upper surface the relatively weak development of sori is seen both in the narrower and broad zones. The frond is 2-layered for about 1 cm. below the up-curled apical part, and the rest of the frond downwards 3-layered. In the arrangement of the piliferous bands, cell-size in the three layers, and mode of development of the frond from the row of apical cells, there is agreement with the oogonial plants described above.

The sori are raised a little above the surface of the frond and form continuous or interrupted bands, 100 to 350 μ wide, the margins of the bands being jagged. The bands of sori arise successively in a zone; thus young and also empty sori may be seen side by side. The antheridia are oblong or square in surface view of the frond and are arranged in close, longitudinal rows (Fig. 5). In the case of the lower surface of the frond, the longer cells of the area forming a sorus divide by a transverse wall into two antheridial mother-cells, thus the range in length of the antheridial mother-cells is 17.5-28.0 μ, whereas that of the lower surface cells is 21-42 μ. When a sorus is formed on the upper surface of the frond the longer cells divide by 1 to 3 transverse walls forming 2 to 4 antheridial mother-cells, evidence of this being seen in old sori after the antheridia have disappeared (Fig. 16, *tw*). The width of the superficial cells forming the antheridial mother-cells remains the same normally, but exceptionally there is a division by a sagittal wall (Fig. 13, *ns*). The antheridial mother-cells develop from the superficial cells by increase in height. In each mother-cell a periclinal (frontal) wall then cuts off a low basal cell having the same width and length as the mother-cell. In height the antheridia are



FIGS. 9-16. *Padina gymnospora* (Kuetzing) Vickers

9. T. S. frond with oogonial mother-cells. 10. Sagittal section frond showing oogonial sorus and portion of empty adjoining sorus on either side. 11. Sagittal section frond with oogonial sorus. 12*a*. Uppermost layer of frond in sagittal section with young piliferous band. 12*b*. Proliferation at base of segment of hair, of piliferous band. 13. T. S. frond showing antheridial sorus. 14. Sagittal section frond with antheridial sorus on upper and empty antheridial sorus on lower surface. 15. Sagittal section frond showing indusium over empty antheridial sorus. 16. Upper-surface cells of frond showing 2 or 4 basal cells after break-down of antheridia.

a-antheridium. *abc*-antheridial basal cell. *eas*-empty antheridial sorus. *eos*-empty oogonial sorus. *eo*-empty oogonium. *fw*-frontal wall. *i*-indusium. *im*-indusial margin. *ll*-lower layer. *lml*-lowermost layer. *ml*-middle layer. *ns*-new sagittal wall. *nw*-new wall. *o*-oogonium. *obc*-oogonial basal cell. *om*-oogonial mother-cell. *ow*-old wall. *sc*-subsidiary cell. *sw*-sagittal wall. *tw*-transverse wall. *ul*-upper layer. *uml*-uppermost layer. *uom*-undeveloped oogonial mother-cell. *yh*-young hair.

one and a half to twice their width, the height 17.5-35.0 μ, width 12.0-24.5 μ. The height of the basal cells is 10.5-17.5 μ. The antheridia of the lower surface are mostly shorter than those of the upper surface, though the length-range is the same. The antheridial sori do not show the presence of an indusium usually (Figs. 13 and 14), but in exceptional cases an indusium is seen (Fig. 15, *i*). The sperms are liberated by the walls of the antheridia and sperm mother-cells dissolving. Subsequent to the liberation of the sperms the sori appear as depressed areas on the frond, as the height of the basal cells is less than that of the general cells on either surface. The antheridium has in surface view of the frond, usually 16 to 32 sperm mother-cells with very delicate walls, 32 to 40 in transverse and sagittal sections ; thus there are about 128 to 320 sperm mother-cells in an antheridium. It is probable as has been demonstrated by Williams (1897, pp. 547, 548 and 552) in allied genera that the sperms of *Padina* are produced singly in the sperm mother-cells and are motile.

The following specimens are preserved in the Herbarium of the Central Marine Fisheries Research Station, Mandapam Camp : Puthumadam—No. 501, 31-1-1952, Oog. No. 1012, 6-1-'53, Anth. (piece only). No. 1013, 29-1-'53, Anth. No. 1014, 29-1-'53, Oog. No. 3212, 29-10-'57, Oog. (piece only). No. 3213, 29-10-'57, Oog. Krusadi I : No. 3214, 14-11-'57, Oog. Pamban Town : No. 3215, 16-11-'57, Oog. Mandapam Camp (Palk Bay) : No. 8001 (4 plants), 24-4-'59, Oog.

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SUMMARY

The gametophytes of *Padina gymnospora* (Kuetzing) Vickers are far from well known. It was possible to obtain ten oogonial and two antheridial plants in the Mandapam area. The antheridial plant is being reported for the first time. The frond structure in the two phases of the gametophytic generation of this species is found to agree with that of the sporophyte. A peculiarity in the structure of the hairs in the species, noticed in the present material, has been described. Germination *in situ* was seen, and a few oogonial sori were found to show the presence of the subsidiary cell. A few of the hairs of the piliferous bands of the frond, in one case, were seen to give rise to a propagule which was terminally or laterally placed on the hair. The evidence that the gametophytic generation of *P. gymnospora* (Kuetzing) Vickers has unisexual plants proves that it is distinct from *P. australis* Hauck, a species having a bisexual gametophyte, which was synonymised with it. Observations indicate the existence of periodicity in the development of gametes in *P. gymnospora* (Kuetzing) Vickers.

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