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DEVELOPMENTAL MORPHOLOGY OF *LAMPROTHAMNIUM PAPULOSUM* (WALLR.) J. GROVES AND *LAMPROTHAMNIUM SUCCINCTUM* (A. BR.) R. D. WOOD[1,2]

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ABSTRACT

Developmental morphology of a monoecious conjoined (*L. papulosum*) and a sejoined species (*L. succinctum*) of *Lamprothamnium* has been studied. In the structure of the node of the axis as well as the basal node of the branchlet and in the origin of stipulode and the sex organs, *Lamprothamnium* shows a distinct difference from similar organs found in *Chara* and the other members of the Chareae. From a study of the structure and development of *Chara succincta* it is clearly evident that it properly belongs to *Lamprothamnium*.

INTRODUCTION

The type of genus *Lamprothamnium*, as orginally demarcated, is similar to *Chara* but differs essentially in the arrangement of sex organs. In a conjoined condition the oogonium is below or by the side of the antheridium, a condition reverse or different to that seen in *Chara* . It has a single stipulode opposite to each branchlet. The oogonium has globular coronal cells and the shoot apex gives a fox-tail appearance.

Ophel (1947) transferred *Chara macropogon* A. Braun to *Lamprothamnium* as it resembled the latter in vegetative features.

In dealing with sejoined species, Wood (1962) followed Ophel and transferred *C. succincta* Braun to *Lamprothamnium* as it resembles the latter in all the other features. Similar transfers of certain dioecious species of *Chara* and *Nitellopsis* were made by Daily (1967).

One main problem posed to the taxonomist is the status of sejoined species of *Lamprothamnium* and the extent of importance one can attach to the sex organs and vegetative features. One way of solving this problem is to base our judgment on a study of the origin and development of sex organs and other vegetatative structures in the type species, viz. *L. papulosum* and in the later erected species, viz., *L. succinctum*. We have only a fragmentary knowledge of the developmental morphology of *L. papulosum* and *L. succinctum* and this is on the basis of studies carried out by Giesenhagen (1896) and Iwasaki (1963) respectively. In the present study a detailed account of the

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developmental morphology of both species has been carried out based on specimens maintained in cultures.

MATERIALS AND METHODS

Live specimens of *L. papulosum* were obtained from Prof. Langangen of Norway. They were grown in 250 ml conical flasks containing autoclaved soil and water (Imahori and Iwasa, 1965).

Dixit (1931), Sinha and Noor (1967) and Sinha and Verma (1970) have reported the occurrence of *L. succinctum* in India as *C. succincta* (See Khan, 1980). Srinivasa Rao and Leelawathi (1979) also reported of the occurrence of *C. succincta* in the Pulicat Lake, near Madras. This material on examination has been found to be *L. succinctum.* The live material of *L. succinctum* was collected from the brackish water lake, viz., Pulicat Lake, sixty miles north of Madras on 18.3. 1979. Live specimens were brought to Madras and have been successfully grown in the above-mentioned medium. The cultures were provided with three cool-day-light Philips fluorescent lamps with approximately a light intensity of 1500 Lux. The cultures were kept in air-conditioned chamber where the temperature was maintained at 25° ± 2°C.

Apices along with 2 or 3 nodes were cut and fixed in Nawaschin's fluid for 24 hours. Microtome sections were taken at 10 μm thickness by following the coventional dehydration and paraffin infiltration technique. Sections were stained in Heidenhain's iron-alum haematoxylin, dehydrated, cleared in xylol and mounted in DPX mountant.

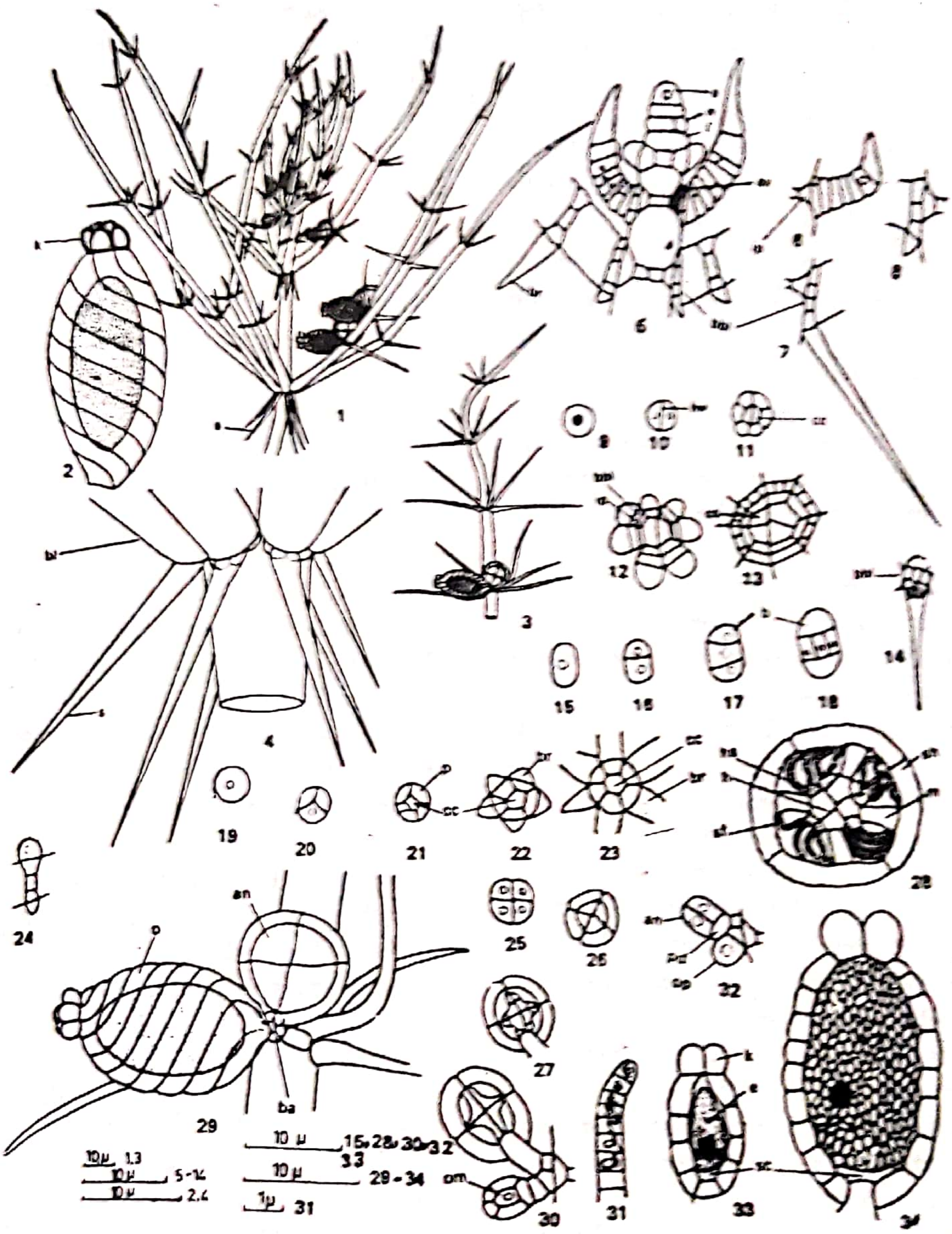
The taxonomic characters of the specimens of both the species grown in the laboratory were verified with descriptions from monographs (Pal *et al.*, 1962; Wood and Imahori, 1965).

Lamprothamnium papulosum (Wallr.) J. Groves (Figs. 1-34, 79, 82, 83, 85, 89).

The main axis: The main axis exhibits an unlimited growth. The growth of the main axis is by means of a dome-shaped apical cell, which is 30 to 40 μm in diameter at base and 35 to 45 μm in height (Fig. 5). It cuts off continuously transverse segments below, each of which divides transversely into an upper nodal and a lower internodal cell. The nodal initial by undergoing a series of vertical divisions differentiates into a node consisting of a central pair of cells, surrounded by 6 to 7 peripheral cells (Figs. 9-13).

The nodal initial divides first by a 'halving wall' (Fig. 10) and the peripheral cells are formed by the formation of curved septa in alternate sequence, the successive divisions being formed in a plane intersecting the preceding planes of division (Fig. 11). Each of the central cells, divides into two cells, so that four central cells are present in a node (Figs. 13, 82). Rarely further divisions may take place in the central cell so that the number of central cells may be more than four.

Branchlet : The peripheral cells of the nodes are responsible for the formation of branchlets. Initially, each peripheral cell (branchlet initial cell) protrudes and divides into an outer and inner cell by a periclinal wall (Figs. 12, 79). Of the two cells thus formed, the outer cell functions as the apical cell of the branchlet. After cutting off 3 to 4 segments it ceases to divide further and assumes an elongated appearance (Fig. 6). Meanwhile, the inner cell by a periclinal division forms the upper basal nodal cell and the lower primary internodal cell of the branchlet (Fig. 12). Each of the segments above the basal node divides transversely into two cells,



Figs. 1-34. *L. papulosum.*

1. A portion of the plant maintained in Culture. 2. Oogonium. 3. Branchlet node with ooganium below antheridium. 4. Axis node with stipulodes opposite to branchlets. 5. L.S. of the apex. 6. L.S. of young branchlet. 7. L.S. of axis node showing stipulode. 8. T.L.S. of the basal node. 9-13. Stages in the development of axis node in T.S. 14. Basal node of the branchlet with stipulode. 15-18. Stages in development of basal node of the branchlet. 19-23. T.S. of branchlet node. 24. T.S. of the branchlet node showing first division of the peripheral cell. 25-28. Stages in development of antheridium. 29. Branchlet node dissected out to show the basal node of antheridium. 30. and 32-34. Stages in development of oogonium. 31. Supermatogenous filaments with supermatozoids. (an=antheridium; br=bract; cc=central cell; e=egg cell; h=primary head cell; hs=secondary head cell; k=coronal cells; m=manubrium; o=oogonium; om=oogonial mother cell; Op=oogonial primordium; p=peripheral cell; pd=pedicel; sc=sterile cell; sf=spermatogenous filaments; sh=shield cell).

the upper nodal initial and the lower internodal cell. The division of the segments of the young branchlet into the nodal and the internodal cells starts at the base of the branchlet and proceeds upwards (Fig. 5) similar to the condition seen in *C. delicatula* and unlike in *C. zeylanica* (Sundaralingam, 1954).

By a series of vertical curved septa, the branchlet nodal initial forms a node consisting of four or five peripheral cells enclosing a single cell in the centre (Figs. 19-23). The peripheral cells in the branchlet nodes are cut off as soon as each of the primary segments of the branchlet divides into the nodal and the internodal cells. The nodal initial first cuts off a single peripheral cell towards the main axis. Subsequently, cells are cut off alternately to the right and to the left in a plane intersecting the planes of previous divisions (Figs. 20, 21) and finally the central cell is completely surrounded by 4 to 5 peripheral cells (Fig. 21). Each peripheral cell of a branchlet node divides into an outer and an inner cell (Fig. 22). The outer cell grows out into a bract. The inner cell does not divide any further and remains as a basal cell of the bract (Figs. 23, 85). The internodal cells of the branchlet remain ecorticate.

Basal node of the branchlet: The basal node and its development are very characteristic and differ from those of the other nodes of the branchlet. The basal node initial begins to cut off cells before the upper segments of the branchlet divide into the nodal initial and the internodal cells. Giesenhagen (1896) was the only author who had given an account of the development of the basal node of *Lamprothamnium papulosum* (as *L. alopecuroides*).

In the present materail, the basal node initial (Fig. 15) cuts off the first peripheral cell on the side of the main axis (adaxial) by a transverse wall (Fig. 16). Another peripheral cell is cut off on the abaxial side by another wall parallel to the first one (Figs. 17, 83). Then the middle cell divides in to three cells by two longitudinal walls intersecting the two transverse walls formed already. Thus, five cells are formed, one each at adaxial and abaxial sides and three in the middle (Fig 18).

Stipulode: At the base of each branchlet only a single stipulode is formed (Figs. 8, 14). This stipulode arises from the abaxial cell of the basal node. The abaxial cell divides periclinally into an outer and an inner cell (Fig. 8). The outer cell elongates and becomes the long stipulode which points downwards (Figs. 4, 7, 14). The inner cell divides anticlinally to form two cells (Fig. 4).

Axillary branch: In the present material axillary branch is very rarely found. Whenever a branch is formed, it originates from the axil of the oldest branchlet. The starting point of the branch is the primary internodal cell of the branchlet which protrudes upwards and cuts off a single segment below by a transverse wall (Fig. 5) and the development proceeds on the same lines as in *L. succinctum* to be dealt with later.

Gametangia : Lamprothamnium papulosum is monoecious. Sex organs are borne generally on the lower two nodes of the branchlet. The oogonium is below the antheridium (Fig. 3), (or somewhat lateral) a feature characteristic of *Lamprothamnium,* as orignially described.

The oldest peripheral cell of the branchlet node, (facing the main axis) by further divisions, form the antheridial and the oogonial primordia. To start with, this cell divides, into an outer and an inner cell (Fig. 24). The inner cell divides again by a wall parallel to the previous one into two cells, so that a row of three cells is formed. The outermost cell is the antheridial primordium while the middle cell is of the nature of the node which by anticlinal divisions froms five peripheral cells round a central cell. Of these five cells, the lowermost (the abaxial) cell enlarges and forms the oogonial primordium, while the other cells do not develop further. Thus the developing oogonium comes to be below the antheridium. Sometimes one of the lower (lateral) cells forms the oogonial primordium. Therefore, the developing oogonium appears to be lateral to the antheridium (Figs. 29, 30).

Antheridium : The antheridial primordium cuts off a discoid cell at base (the pedicel cell) and becomes the antheridial mother cell assuming a spherical shape. It divides by a longitudinal wall into two hemispherical cells each of which divides again by another longitudinal wall at right angles to the previous one (Figs. 25, 32). Each of the four quadrants thus formed divides transversely into two cells and eight cells (octants) are formed. Thus, in *L. papulosum* it is octoscutate (Fig. 29). Each octant by two periclinal divisions forms a row of three cells (Figs. 26, 27). In the meantime the pedicel cell protrudes into the cavity of the antheridium (Fig. 30). The 8 outer cells expand to form the shieldcells and the middle cells develop into the manubria and the inner cells form the primary capitula each of which soon cuts off 2 to 4 cells, the secondary capitula. The secondary capitula by further divisions give rise to the spermatogenous filaments (Fig. 28).

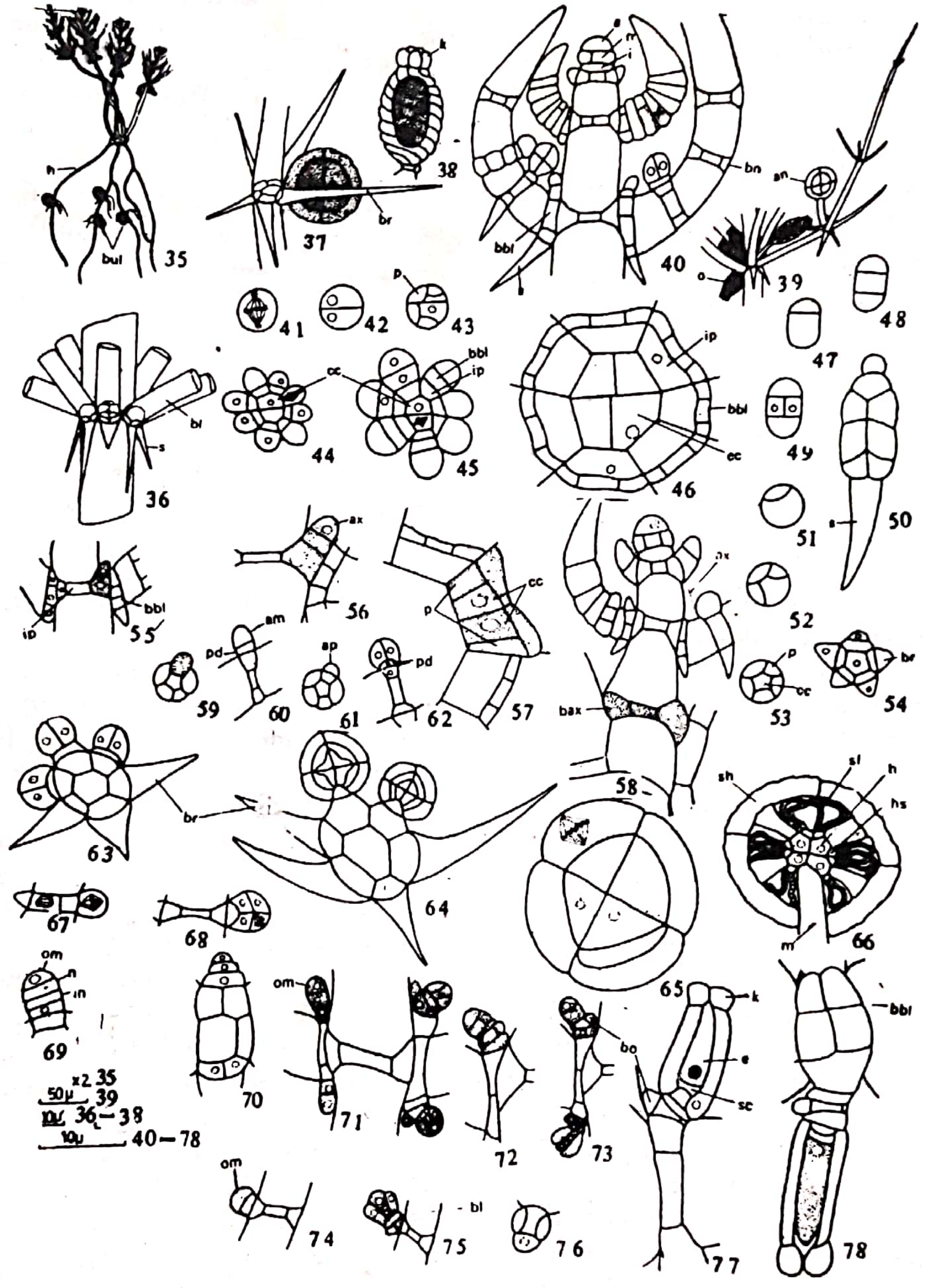
Oogonium : The oogonial primordium divides by a transverse wall to form an outer oogonial mother cell and an inner cell which divides into an upper nodal cell and a lower internodal cell. The nodal cell forms five peripheral cells round a central cell. The peripheral cells elongate upwards and envelop the enlarging oogonial mother cell. Each of the enveloping cells cuts off a cell at the top which becomes globose and forms the crown cell (Fig. 34, 89). The oogonial mother cell in the meantime cuts off a narrow sterile cell at the base and becomes the egg cell (Fig. 33). The enveloping cells coil, the spiral ascending from right to left (Fig. 29). The enlarging egg cell gets filledwith starch grains (Fig. 34).

Lamprothamnium succinctum (A. Braun), R. D. Wood (Figs. 35-78, 80, 81, 84, 86-88).

The growth of the main axis is by means of a domeshaped apical cell, which is 50 to 60 μm in diameter and 100 to 110 μm in height (Fig. 40). The node of the main axis consists of a central pair of cells surrounded by 7-8 peripheral cells (Figs. 41-45,80). Further, the central cells divide to form a four celled formation (Figs. 46, 81) thus agreeing with the pattern seen in *L. papulosum*. But according to Frame and Sawa (1975) only one of the central cells divides thus making up a three-celled central cell complex of the node.

L. succinctum exhibits a basifugal condition of branchlet differentiation (Fig. 40). (See also Iwasaki, 1963). In this it differs from many *Chara* spp. and agrees with the condition seen in *Lamprothamnium papulosum*. The number of peripheral cells cut off in the nodes of the branchlet varies from four to five (Figs. 51-54, 84).

The basal node of branchlet in *L. succinctum* (cf. Iwasaki, 1963) differs some-



Figs. 35-78. *L. succinctum*. 35. Habit of plant from nature. 36. Axis node; 37. Branchlet with antheridium. 38. Oogonium. 39. Axis node with oogonia at the base of the branchlet and antheridium at the branchlet node. 40. L.S. of the apex. 41-46. Developmental stages of the axis node. 47-50. Stages in development of basal node of the branchlet. 51-54. Developmental stages of the branchlet node. 55-58. Stages in development of the axillary branch. 59-68. Stages in development of the antheridium. 69-73, 77 and 78. Basal node of the branchlet forming oogonium. 74 and 75. Development of oogonium from the branchlet node. 76. Basal node of oogonium.

what from that of *L. papulosum.* It cuts off an adaxial cell and an abaxial cell with a middle cell. Thus a row of three cells is formed (Figs. 47, 48, 86). The middle cell divides only once longitudinally into two cells (Fig. 49). Thus, there are only four cells in the basal node and not five as in *L. papulosum.*

The abaxial cell of the basal node of the branchlet in *L. succinctum* gives rise to a stipulode (Figs. 36, 50) in the same manner as in *L. papulosum* (Iwasaki, 1963).

Axillary branch :

As in *L. papulosum* the primary internodal cell of he oldest branchlet grows upwards with a broadly rounded top into the apical cell of the future branch and cuts off a single segment which develops into the basal node of the branch by cutting off 4 peripheral cells around a pair of central cells (Figs. 55-57, 58). The apical cell then continues to cut off segments below, each of which divides by a transverse wall into an upper nodal and a lower internodal cell and further stages of development are very similar to those of the main axis (Fig. 58).

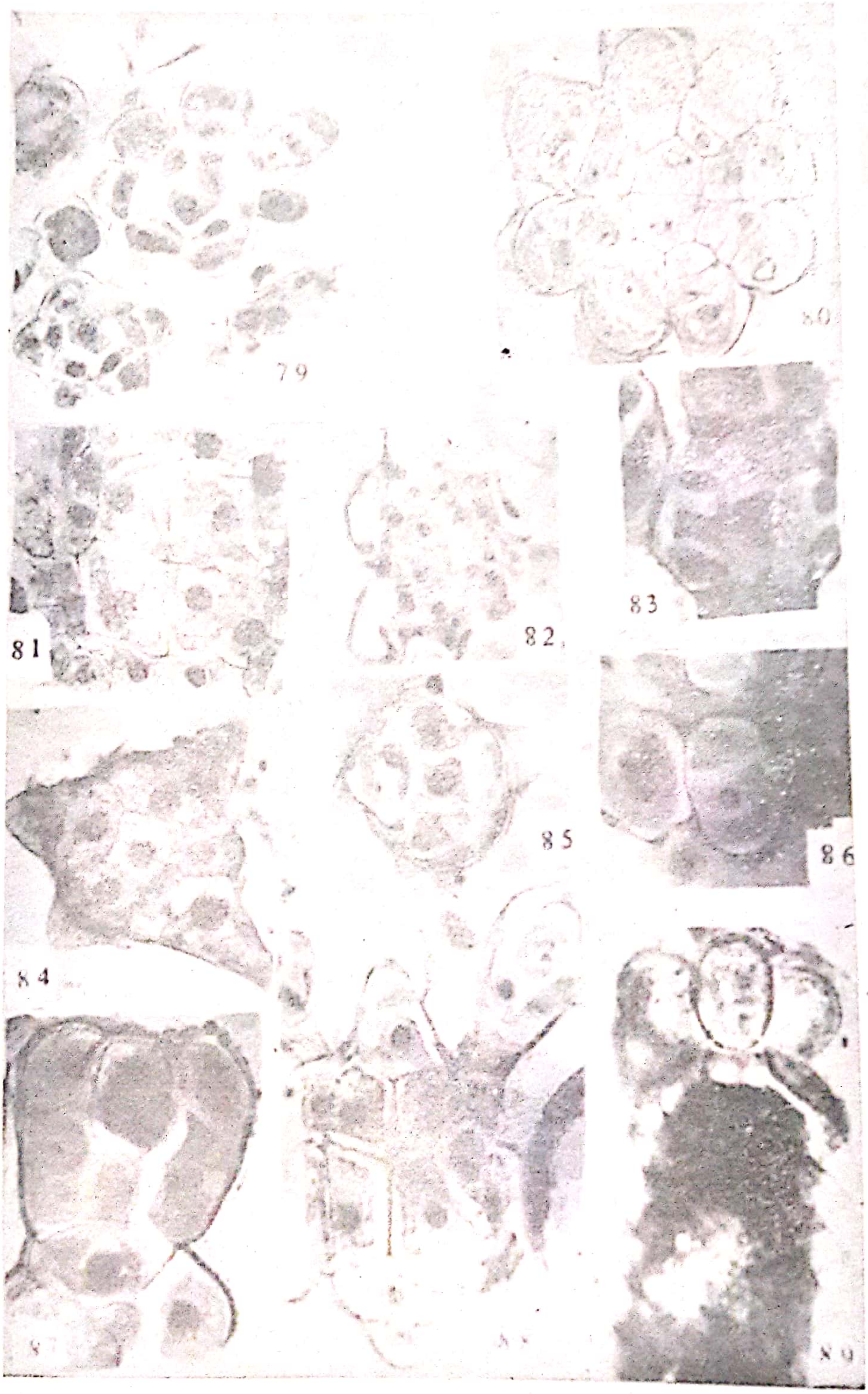
L. succinctum, as in *L. papulosum,* is monoecious but the antheridia, are restricted to the branchlet nodes and the oogonia generally to the base of the branchlets (sejoined condition) (Figs. 37, 39).

The antheridia are formed on the adaxial side of the two lower branchlet nodes of each branchlet. The first (oldest) peripheral cell of the two branchlet nodes facing the main axis gives rise to the antheridium. This adaxial peripheral cell divides tranversely into two cells, of which the inner cell does not divide any further and remains as a basal cell (Figs. 59-61). The outer cell functions as the antheridial primordium, which divides to form the outer antheridial mother cell and a lower pedicel cell (Figs. 60, 67). The antheridial mother cell by two longitudinal divisions and one transverse division reaches the octant stage i. e., the antheridium is octoscutate (Figs. 62, 65, 66, 68). Antheridia were also observed in pairs (geminate) in the same branchlet node (Figs. 63, 64), In such cases, they develop from the first two peripheral cells on the adaxial side of the branchlet.

The oogonium (Figs. 38, 72, 73, 77, 78) in the case of *L. succinctum* develops from the adaxial and/or abaxial peripheral cell of the basal node of the branchlet (Figs. 71, 88). The adaxial or the abaxial cell of the basal node of the branchlet cuts off two segments below and becomes the oogonial mother cell (Figs. 69-71). Of the two segments cut off, the lower segment develops into the basal node of the oogonium (Fig. 77). When the oogonia arise from abaxial cell (s) stipul[illegible]es are not present at the base of the branchlets.

The presence of a basal node below the oogonium (Fig. 78) is peculiar and has not been reported earlier in *L. succinctum* (cf. Iwasaki, 1963). It has however been noticed in dioecious species of *Chara,* e. g., *C. wallichii* (Sundaralingam, 1963). The basal node of the oogonium consists of three peripheral cells with a central cell (Fig. 76). The first peripheral cell protudes in front.

Occasional development of oogonium in place of antheridium from the branchlet node is seen in *L. succinctum* (Figs. 74, 75). Whenever an oogonium is found at branchlet node, it arises from the oldest (adaxial) peripheral cell of the branchlet node.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DISCUSSION

Based on the present study of the type species, a pattern of development characteristic of the genus *Lamprothamnium* is envisioned and an attempt is made to find out how for the other species attributed to this genus share this pattern.

The dome-shaped apical cell is responsible for the unlimited growth exhibited by the main axis. The pattern of growth of the main axis and the branch is more or less similar to that seen in other members of Characeae (Sundaralingam, 1954 and Iwasaki, 1963).

In the structure of the axis node, the number of central cells is considered a critical feature. The pair of central cells of the axis node does not divide in *Chara* (Sundaralingam, 1954, 1963), *Lychnothamnus* (Sundaralingam, 1962) and *Nitellopsis obtusa* (Giesenhagen, 1897, Bharathan, 1983). The pair of central cells in *Lamprothamnium papulosum* and *L. succinctum* divides further. This was also pointed our earlier (Giesenhagen, 1897, Iwasaki, 1963 and Frame and Sawa, 1975). In the present study it was found that in both the species of *Lamprothamnium* the two central cells of the axis node divide to form four cells. Thus, among Charae, *Lamprothamnium* is demarcated from the rest by the anatomy of the axis (Frame and Sawa, 1975). Daily (1980) however does not give taxonomic importance to the range or the number of central cells in the axial nodes.

The peripheral cells of the axis node are responsible for the formation of branchlets through a series of divisions and differentiation. The differentiation of the nodal segment proceeds from base to apex i. e., basifugal or it may start first in the upper-most segment and proceed downwards,i. e., basipetal. In *L. papulosum* and in *L. succinctum* basifugal pattern of differentiation takes place. Existence of a similar condition has already been reported in *C. delicatula*, *Lychnothamnus barbatus* (see Sundaralingam, 1962). It differs in this respect from *C. fragilis*, *C. zeylanica* (see Sundaralingam, 1954), *C. benthamii* and *C. braunii* (Iwasaki, 1962) which show a basipetal condition.

Basal node of the branchlet :

The basal node of the branchlet is one of the important units of the axial node. The taxonomic value of this structure is immense. Therefore the morphology of the basal node of *Lamprothamnium* has been studied very critically. The basal node of *L. papulosum* consists of five cells, with four priphe-

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Figs. 79-89. *L. papulosum* : 79, 82, 83, 85, 89. 79. T.S. of the axis node showing central cells surrounded by peripheral cells (× 200). 82. T.S. of axis node showing 4 central cells (× 400). 83. T.L.S. of the axis node showing 3 celled stage of the basal node of branchlet (× 200). 85. T.S. of branchlet node showing central cell, basal cell of the bract and bract (× 200). 89. Mature Oogonium showing globose crown cells (× 100).

Figs. 80, 81, 84, 86, 88. *L. succinctum*, 80. T.S. of the axis node showing formation of primary internodal cell and basal node of branchlet (× 200). 81. T.S. of the axis node showng 4 central cells (× 200). 84. T.S. o the branchlet node showing central cells, basal cell of the bract and bract (× 200). 86. T.L.S. of the axis node showing 3 celled stage of the basal node of the branchlet (× 160). 87. L.S. of young oogonium showing oogonial mother cell, peripheral cell and basal node of oogonium (× 400). 88. T.L.S. of axis node showing basal node of branchlet developing oogonium (× 400).

ral cells around a central ceell. There are only four cells in *L. succinctum* and the central cell is absent. Both the species differ from *C. zeylanica*, *C. corallina*, *C. hydropitys* (Sundaralingam, 1954, 1963, 1966), *C. benthamii* and *C. braunii* (Iwasaki, 1962, 1963) and *Lychnothamnus barbatus* (Sundaralingam, 1962), due to differences in sequence of cell division and cell arrangements.

Stipulodes :

In *L. papulosum* there is a single row of stipulodes, each opposite and below a branchlet. A similar condition exists in *L. succinctum*. In both the cases the stipulodes develop from the abaxial cell of the basal node of the branchlet. However in *L. succinctum* the abaxial cell produces the oogonium during the reproductive phase. The unistipulate condition in *Lamprothamnium* is diffèrent from that of *C. benthamii* and *C. braunii* (Iwasaki, 1962, 1963).

The Axillary Branch :

Axillary branch is produced from the primary internodal cell of the branchlet. In both the species of *Lamprothamnium* the first division is transverse. Therefore, a small (oblique) segment is not formed on the side of the branchlet unlike the case in *Chara*, *Lychnothamnus* and *Nitellopsis*. The condition in *Lamprothamnium* is therefore similar to that observed in *Nitella* (Sundaralingam, 1962).

Sex organs:

Chareae and Nitelleae are distinguished by the number of their coronal cells. The genera included in these subfamilies were separated on the basis of the relative disposition of the two gametangia in them (Groves, 1924). But the presence of dioecism and the occurrence of sejoined rather than conjoined condition of gametangial arrangement in species created problems (Ophel, 1947, p. 321). The development of gametangia in all monoecious species like *C. zeylanica* (Sundaralingam, 1954) is invariably similar. While in *Chara* the adaxial cell of the basal node of the anteridium forms the oogonium, in *L. papulosum* it is the abaxial cell which develops into the oogonium. In sejoined species like *L. succinctum* the oogonium develops from the adaxial and/or abaxial peripheral cell of the basal node of the branchlet, a condition similar to that seen in dioecious species of *Chara* like *C. wallichii* (Sundaralingam, 1963). In the oogonium of *L. succinctum* a basal node is present below the oogonium. A similar condition was noted in *C. wallichii* (Sundaralingam, 1963). It is absent in *Nitellopsis obtusa* (Bharathan, 1983). The origin of oogonia in *L. papulosum* was found to be clearly distinct from the monoecious members of *Chara*. The development of oogonium from the basal node of the branchlet and that of the antheridium singly or in pairs from the first or from the first and second peripheral cells of the branchlet node is characteristic of *L. succinctum*. In both the species globose crown cells are seen and the antheridia are found to be octoscutate.

Due to the foxtail appearance of the shoot apex, the distinct basal node of the branchlet, the opposite disposition of the stipulode, globose crown cells, Wood's (1964) treatment of *C. succincta* as *Lamprothamnium succinctum* can be considered valid. A similar study on the other species and varieties of *Lamprothamnium* is very essential to find out their taxonomic status.

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