Bulbils of some charophytes

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Abstract. The structure and development of the bulbils of Chara hornemannii, Chara aspera, Lamprothamnium papulosum, Lamprothamnium succinctum and Nitellopsis obtusa have been studied.

Keywords. Bulbils; Chara; Lamprothamnium; Nitellopsis; developmental morphology.

1. Introduction

The process of vegetative propagation through specially organized morphologically distinct bulbil is quite wide spread among the members of Charophyta. In the present study the structure and development of bulbils of Chara hornemannii, C. aspera, Lamprothamnium papulosum, L. succinctum and Nitellopsis obtusa have been carried out in detail based on all these specimens obtained from cultures maintained in the laboratory.

2. Material and methods

Live specimens of C. hornemannii Wallm. were obtained from Prof. Proctor (Texas, USA). C. aspera Wild. and L. papulosum (Wallr.) J. Groves were sent by Prof. Langangen of Norway. L. succinctum (A.Br.) RDW was collected from Pulicat lake, 60 miles north of Madras. Specimens of N. obtusa (Desv.) Groves were received from Prof. Willén (Sweden). All the specimens were grown in the laboratory (Bharathan 1983; Bharathan and Sundaralingam 1984) and bulbils required for observation were taken from the cultures at different stages. The bulbils were kept in petri-dishes containing sterilised water and they produced new plants within 3–5 days. The sprouting bulbils were observed at different stages of their development. The morphology of the bulbils were studied by direct observations under stereo-dissection binocular microscope and with the help of serial microtome sections.

3. Observations

3.1 C. hornemannii

3.1a The structure of the bulbils: The bulbils make their appearance when the vegetative growth of the plant reaches its maximum level. The bulbils develop from the extensively growing larger rhizoids. These rhizoids develop from the lowermost, swollen, underground node of the plant. The bulbil-forming rhizoids are 200–250 μm in diameter and are repeatedly branched at the regions of the S-shaped oblique cross walls (double footed joint according to Groves and Bullock-Webster 1924).
As in secondary rhizoid formation, a S-shaped oblique wall is formed (figure 1) and at the lower part of the oblique wall a cell is cut off by the formation of a cross wall. The newly formed cell divides by a longitudinal and a transverse wall, forming 4 cells (figure 2). Each of these cells develop a secondary rhizoid. But during bulbil formation, one or two of the 4 cells enlarge to develop into a single or a pair of globose bulbils (figures 3–5).

3.1b Sprouting of the bulbil: The globose bulbil gradually enlarges, fills with starch grains and forms a few cells at both ends. To start with it cuts off a cell at the top, which divides into 6 to 7 cells, often arranged with two cells in the centre and 4 or 5 cells around resembling a node (figure 9). Under favourable conditions, some of the peripheral cells cut off segments towards outside, which grow out into the protonemata (figure 6).

The young protonema enlarges and cuts off an apical cell by a transverse wall. This apical cell cuts off, at its lowerside, 3 to 4 cells in a row (figures 10–12). These cells form the terminal process of the protonema. In this manner, on both ends of the bulbil, 3 or more protonemal processes are produced (figure 6). Further development of the protonema and the formation of a new plant from the bulbils (figures 7, 8 and 14) are similar to the pattern observed during the oospore germination (Sundaralingam 1954).

3.2 C. aspera

The lowermost node of the main axis of C. aspera forms an irregular mass of cells. From this mass a few rhizoids are produced which penetrate deep into the soil and form globose bulbils (figure 15) at the S-shaped cross wall regions. The bulbils are generally seen in pairs and their development and sprouting pattern are similar to those of C. hornemanni.

3.3 L. papulosum

The bulbils of L. papulosum (figure 16) are similar to those of C. hornemanni. The rhizoids at the region of S-shaped cross walls bear bulbils. The bulbils are globose, 2 to 3 mm in diameter and completely filled with starch grains. The starch grains are discoid in shape.

3.4 L. succinctum

The bulbils of L. succinctum (figure 17) are similar to those of C. hornemanni. They bear globose bulbils which are 5 mm in diameter.

3.5 N. obtusa

3.5a The structure of the bulbil: The bulbils of N. obtusa are borne on the main axis below the soil and they represent the condensed nodes. The branches of the main axis below the soil grow downward (positively geotropic) forming bulbils at each
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Figures 1-17.

1. Rhizoid showing S-shaped oblique wall.
2. Rhizoid showing 4 cells above the S-shaped oblique wall.
3-5. Development of bulbil near the S-shaped wall of the rhizoid.
7. Bulbil showing protonema with the terminal process, rhizoid node and branchlet node.
8. Development of adult plant from the protonemal branchlet node.
9. LS of the bulbil showing cluster of cells at the apex and starch grains in the bulbil.
14. Sprouting of bulbil showing development of adult from the branchlet node.
15-17. Stages in development and sprouting of bulbils of C. hornemannii.

15. C. aspera.
16. L. papulosum.
17. L. succinctum.

(Abbreviations: bul, bulbils; pbn, protonemal branchlet node; prn, protonemal rhizoidal node; rh, rhizoid; tp, terminal process.)
Figures 18–27. For caption, see p. 261.
node. The network of branches formed by the axis node is seen just 3 to 4 cm below the surface of the soil, around the growing plant. Most of the bulbils occurring below the soil sprout and produce many plants around the adult plant.

The different stages of development of the bulbils (figures 18–27) can be traced by observing the downwardly growing axis, from its apical region. The axis node initial cuts off 5 to 7, peripheral cells and each one of the peripheral cell forms a branchlet with two or three segments (figure 23). The lowermost segment of a branchlet divides into two viz the inner primary internodal cell and the outer basal nodal cell (figure 25). The inner primary internodal cell enlarges and divides once or twice vertically. The outer basal nodal cell divides to form 8 cells arranged in two rows as in the basal node of the normal branchlet. Each one of the cells above the basal node may also divide to form the upper nodal and the lower internodal cells. The central cells and the primary internodal cells of the axis node become swollen, packed with discoid starch grains and form the middle part of the mature bulbil (figures 18, 19). The branchlets of an axis node constitute the radiating arms of the bulbils and they are very much swollen, short in length and packed with starch grains. Thus, the mature node (bulbil) appears like a star (figures 18, 20).

3.5b Sprouting: As in the case of the axes growing upward, the primary internodal cells of the oldest and next oldest branchlet are responsible for the origin of new plants from the bulbils. These primary internodal cells produce branch initials at a very early stage of development of the bulbil (figure 26). Along with the developing bulbil the branch initials also grow upward and produce new plants (figure 27).

4. Discussion

In the present study two types of bulbils are described i.e. the globose type and star-shaped type. The former is seen in *C. hornemannii*, *C. aspera*, *L. papulosum* and *L. succinctum* and the latter in *N. obtusa*. However, from the materials collected from Allahabad, bulbils were observed by Ramakant and Pandey (1985) in *N. obtusa*. Globose bulbils are produced at the S-shaped cross wall region of large rhizoids. It is similar in structure in all the 4 species viz *C. hornemannii*, *C. aspera*, *L. papulosum* and *L. succinctum*. The present study confirms the earlier observations of Giesenhagen (1896) and McNicol (1906). The bulbils appear like a swollen internode with nodes on either sides. During sprouting, new plants are formed by protonema formation as in oospore germination in *Chara* (Sundaralingam 1954).

The nature of bulbils can also be taken as an important taxonomic character.

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**Figures 18–27.** Bulbils of *N. obtusa*. 18 and 19. Dorsal and ventral view of a fully developed bulbil showing central cell being surrounded by peripheral cells (=primary internode of the branchlet) and condensed branchlets. 20 and 21. Dorsal and ventral view of bulbil in early stage of development. 22–24. Lateral and ventral view of bulbil in still earlier stage of development. 23. Apical region of downwardly growing axis. 25. LS of the downwardly growing young axis node. 26. LS of the downwardly growing young axis node showing formation of axillary branch from the primary internodal cell of the branchlet. 27. Bulbil with adult plant.

*Abbreviations: a, apical cell; ax, axillary branch; bb, basal node of branchlet; cc, central cell; ip, primary internodal cell.*
Zaneveld (1940) used the presence or absence of bulbils as a distinguishing character in some cases. For instance he pointed out that *C. connivens* is distinguished from *C. fragifera*, apart from other characteristics, by the absence of bulbils in the former. In the same way he indicated that *C. aspera* can be recognised by the presence of bulbils on its lower nodes, which feature does not occur in any other dioecious triplostichous *Chara* from Malaysia.

A majority of the bulbil producing plants are found to be dioecious in nature (e.g. *C. hornemannii, C. aspera, C. canescens, C. fragifera* and *N. obtusa*).

Less number of oospores are produced in dioecious taxa of Characeae than in the monoecious taxa. In *N. obtusa* (Olsen 1944) and in *C. aspera* (Daily 1958; Langangen 1974; Croy 1982) it has been pointed out that not only the fructifications are scanty but also the ripe oospores are rarely formed. In *C. hornemannii* and also in *C. aspera* the percentage of germination of oospores is very low (Proctor 1967). Probably the bulbils in these taxa ensure their survival.

The environment seems to play a significant role in the formation of bulbils in most of the taxa. *N. obtusa* resorts to oospore formation at eutrophic conditions (Krause 1985). Usually, *N. obtusa* has been reported to occur at deep water, low water velocity and at low light transmittance (Mukerji 1932; Schloesser et al 1986). In this species Langangen (1974) also has pointed out that the fructification frequency in a lake decreases with increasing depth.

The mode of reproduction viz propagation through bulbils or reproduction by oospores, appears to play a significant role in the distribution of the taxa.

Due to their position in the plant body the oospores have better mode of dispersal than bulbils which occur below the soil. The lack of dispersal mechanism may ultimately lead to an endemic distribution of the given species (Croy 1982). Clones of *C. aspera* from N. America and Europe have shown not only considerable variations but also remained sexually isolated. According to Croy (1982) the reproductive isolation among the plants of the land masses may be due to sporadic gene flow at an earlier date when climate was more favourable for oospore formation.

While oospores have dormant period, varying from one to three months (Proctor 1967; Forsberg 1965) bulbils have no such dormant period. But, at the time of germination of the oospores and at the time of the development of a new plant from the globose bulbils a similarity has been observed. In both these cases initially there is a protonemal formation from which ultimately the new plants are developed. However, the protonemal phase is lacking in the star-shaped bulbils of *N. obtusa* where new plants are directly produced.

Generally, taxa occurring in a given habitat multiply through bulbils have uniformity in their characters than those which produce oospores. Probably, it is this lack of variation which would have led to the similarities between the lime-shells of the ancient species and the present day *N. obtusa* (Daily 1973).

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