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EVOLUTION OF SEX ORGANS AND OOGAMY IN CHAETOPHORALES[1]

BRAJ NANDAN PRASAD

Department of Botany, Lucknow University, Lucknow

ABSTRACT

The paper traces the various stages and steps, as exhibited by various genera, in the evolution of oogamy within the Chaetophorales. The sequence of changes in the sex-organs has been traced leading upto the climax stage found in *Coleochaete*. Their evolutionary and phylogenetic significance has been discussed.

Barring certain select groups *e.g.* the order Oedogoniales, the oogamous genera of Chlorophyceae occupy a more or less isolated position. This is especially true for *Coleochaete* de Brebisson which exhibits the climax stage in advanced oogamy and has moved even higher in evolving the development of a fruit-body or spermocarp with sterile cortications formed as a post-fecundation growth of tightly enveloping investment produced by the adjoining cells or filaments. The oogamy of *Coleochaete* appears striking, in view of the fact that many seemingly more vegetatevely specialised genera of Chaetophorales (Fritsch, 1935), like *Fritschiella*, *Draparnaldia* and *Draparnaldiopsis* have remained at the relatively primitive level of isogamy or anisogamy in their mode of sexual reproduction.

The antheridia and oogonia of *Coleochaete* are highly specialised structures modified and clearly distinct from vegetative cells and are in sharp contrast to the gametangial cells of most other genera of Chaetophorales, wherein the ordinary, unmodified vegetative cells (sometimes in special positions) function as the gametangia. This latter feature is reminiscent of, and akin to, the state attained by *Ulothrix* and its various allied genera. It is tempting to trace the evolution of the specialised sex organs and of oogamy in Chaetophorales culminating in the condition attained by *Coleochaete* which, in respect of sexual apparatus and mechanism, is the climax genus of the entire order. Certain recent findings have made this possible and, in the present communication, an attempt is being made towards its elucidation and indication of evolutionary trends within Chaetophorales in the direction of developing advanced oogamy.

The gamete-producing parent cells of most genera of Chaetophorales are ordinary vegetative cells and there is no differentiation between antheridia and oogonia separately, while in *Coleochaete* they are distinct, specialised structures.

ANTHERIDIA

The male gametangia of most chaetophoralean taxa are unmodified vegetative cells in which the protoplast, after repeated divisions (or otherwise), gives rise to the male gametes. The external form of antheridia among some Chaetophorales appears to have undergone specialisation. *Aphanochaete* and *Chaetonema*, in contrast to Chaetophoralean taxa other than *Coleo-*

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chaete, show a marked differentiation of antheridia. In the former genus, they are small, usually almost colourless and are produced terminally (Fig. 1). It is thus, at the same evolutionary level as the terminal antheridia of most *Coleochaete* spp. in being specialised and is an advanced structure in comparison to the an theridia of *Awadhiella* which are like unmodified vegetative cells. The genus *Chaetonema*, on the other hand, possesses antheridia "formed by transverse and longitudinal division of vegetative cells" into usually eight cells (Fig. 2). These antheridia are altogether unique among the green algae and are comparable to the plurilocular gametangia of the Phaeophyceae. It is tempting to visualise that, if in course of evolution, the outer cells of it were to become sterile, we would get a typical antheridum of a Bryophyte. There is no way, at present, of ascertaining whether this was actually the course of evolution of the antheridium of land plants. The direct derivation from *Chaetonema*, however, seems doubtful as this is a specialised genus. It is more plausible that ancestors of *Chaetonema* possessing similar antheridia were more in the direct line.

In the genus *Awadhiella* (Prasad and Asthana, 1979), antheridia are normally terminal in position (Fig. 3) but may, occasionally, be inter-calary. However, they are always unmodified vegetative cells and there is no evidence that they are especially produced as male gametangia. This condition is reminiscent of of the Chaetophoreae. But, in *Awadhiella*, eight antherozoids are produced per antheridium. Thus, at the level of *Awadhiella*, the form of the male gametangium has remained primitive and unspecialised but the function has pro gressed. However, the production of eight antherozoids is still a primitive feature in comparison to species of *Coleochaete*, in all species of which, only one antherozoid is produced in each antheridium (Fritsch, 1935).

The heterotrichous pulvinate species of *Coelochaete* possess small-celled, especially cut out antheridia which are formed in terminal or lateral positions but are not normally produced in intercalary positions (Fig. 4). In some prostrate, discoid and specialised species (*C. scutata*) of the genus, however, the antheridia are intercalary (Fig. 5). In *C. nitellarum** and *C. pseudosoluta*, they may be terminal (Fig. 6) as well as intercalary (Fig. 7). These latter species possess only prostrate filaments which are rather loosly aranged and are not laterally coalesced firmly to form a compact pseudo-parenchymatous disc similar to those of *C. scutata* or *C. orbicularis*. Evidence has been produced (Prasad and Asthana, 1977) to show that in *C. nitellarum* the antheridia may be produced in basipetal succession resulting in a series of antheridia, the later-formed of which occupy an intercalary position (Fig. 8). In some cases, they may be formed in truly intercalary positions and are bordered on both sides by vegetative cells only (Fig. 7). It is worth noting that such intercalary positions are characteristic of the antheridia of truly discoid species which are considered more specialised and hence more advanced than the pulvinate and heterotrichous species (Fritsch, 1935). Thus, there appears to have been a gradual shifting of the antheridia from terminal or lateral to intercalary positions in the genus *Coleochate*. In some cases, this seems to have gone hand in hand with the aggregation of antheridia but this tendency towards bunching has not progressed very far. In others (*C. pulvinata*),

*Sarma and Chapman (1974, 1975) consider *C. nitellarum* Jost to be *Coleochaete leve*. The present author does not agree with such treatment.

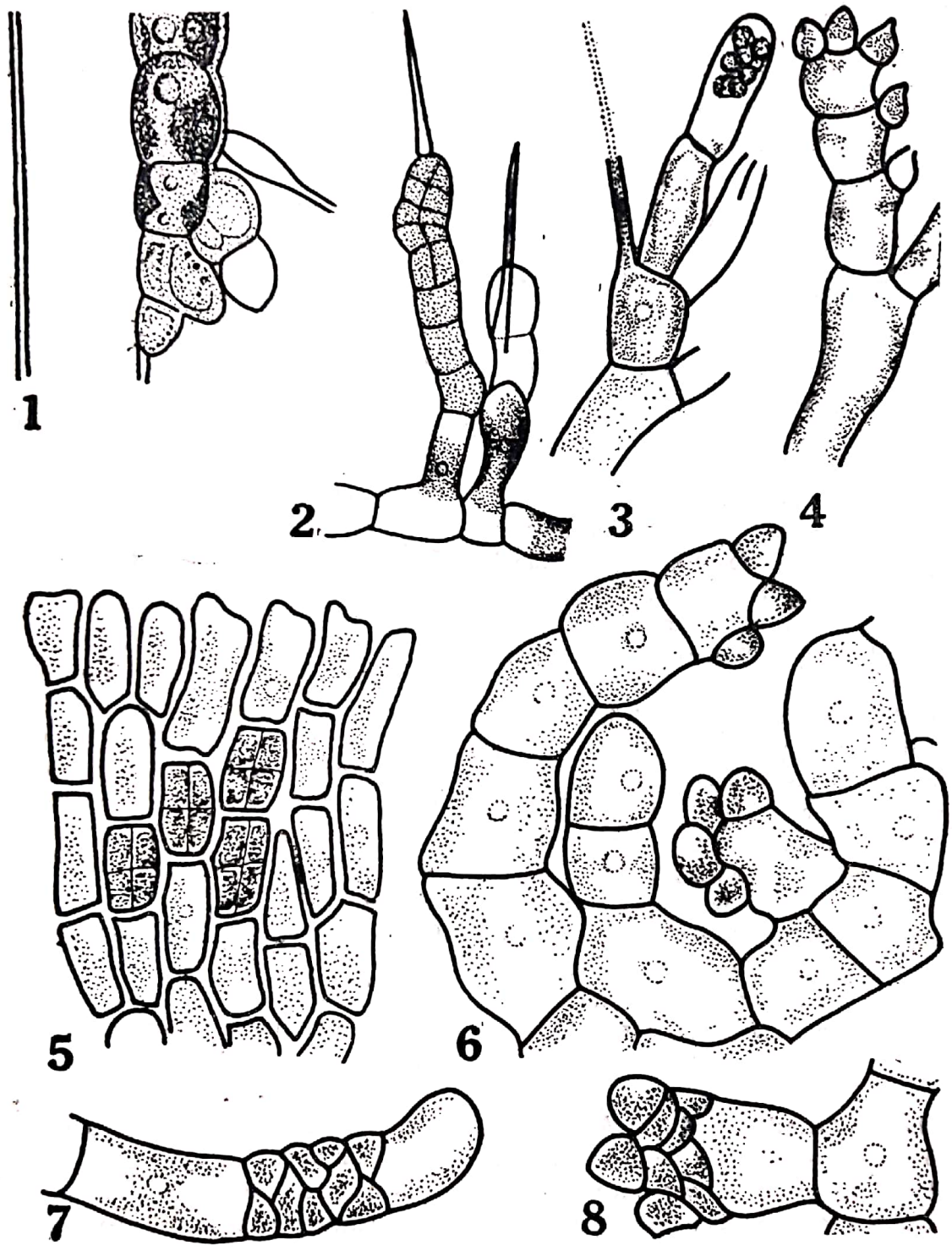

Fig. 1. Antheridia of *Aphanochaete*. Fig. 2. Multicellular antheridia of *Chaetonema*. Fig. 3. Antheridium of *Awadhiella* containing eight antherozoids. Fig. 4. Terminal antheridia of *Coleochaete pulvinata*. Fig. 5. Inter-calary antheridial cluster of *Coleochaete scutata*. Fig. 6. Terminal antheridia of *Coleochaete nitellarum*. Fig. 7. Inter calary antheridia of *C. nitellarum*. Fig. 8. Terminal and centripetally-produced antheridia of *C. nitellarum*.

clustering of antheridia seems to have been achieved independently.

In many of the discoid prostrate species, the antheridia are initially formed at the margins of the discs which are comparable to the terminal positions of the pulvinate species. It is only in the specialised discoid species (*C. scutata*) that the antheridia do not originate at the margins of the disc but arise "from some of the products of division of an intercalary cell' (Fritsch, 1935); they may often occur in clusters. Such "internal antheridia" (cf. Prasad and Asthana, 1977) are of co-ordinate rank to the sub-terminal or intercalary antheridia found in certain species (*C. nitellarum*).

It may be concluded from the observations made above that the terminal antheridia are primitive and the intercalary positions are secondary and relatively more advanced. *Awadhiella indica*, *Aphanochaete* spp. *Chaetonema* spp. and all heterotrichous species of*Coleochaete* possess the primitive type of antheridium; the loosely branched, non-compact and non-discoid prostrate species like *C. nitellarum* and *C. pseudosoluta* show intermediate and transitional stages where antheridia are usually terminal but may be intercalary; and finally, the compact discoid species show the climax stage wherein the antheridia are produced in intercalary positions and are oftenin clusters or bunches.

OOGONIA

Besides *Coleochaete* and *Awadhiella*, only two other genera of Chaetophorales viz. *Aphanochaete* and *Chaetonema* have attained a level of sexual reproduction higher than isogomy and anisogamy which are characteristic of most of the genera. *Aphanochaete* produces distinct, swollen oogania (Fig. 9) as lateral or intercalary structures within each of which, a single, motile, quadriflagellate macrogamete is organised and is liberated out, so that fertilization occurs in the surrounding waters. This is strictly the level of heterogamy where the female gamete is also a swarmer and has not attained the specialisation of an immotile oosphere. In *Chaetonema*, the oogonia (Fig. 10) are distinct and each forms a single egg (oosphere) which is immotile and devoid of flagella but is still expelled or discharged out (Fig. 11), so that fertilization occurs outside the oogonium. *Chaetonema* has, thus, attained the level of 'primitive oogamy' and is more advanced than *Aphanochaete* in its mode of sexual reproduction. It is, however, noteworthy that in both genera, the entire contents of the oogonia are utilised in the organisation of the single mega-gamete and no residual protoplast is left behind.

The genus *Awadhiella* marks an advance over the above-mentioned two genera in that the oogonia here are terminal; intercalary oogonia are rare. No oogonia have been found in lateral positions in this genus so far. *Coleochaete* spp. also possess terminal oogonia; the phenomenon of their subsequent displacement to a lateral position by the formation and growth of a branch from the underlying cell is apparently a subsequent specialisation. *Awadhiella* shows further advance over *Aphanochaete* and *Chaetonema* in that the egg is immotile, is not expelled out of the oogonium and is retained so that fertilization occurs within the oogonium. Hence, *Awadhiella* has reached the level of advanced oogamy.

The genus *Awadhiella*, however shows two features which may be considered more primitive than the position obtaining in *Aphanochaete*, *Chaetonema* and *Coleochaete*. One feature is the frequent formation of two eggs within one oogonium (Figs. 12 & 13), a character which is more primitive than any other oogamous

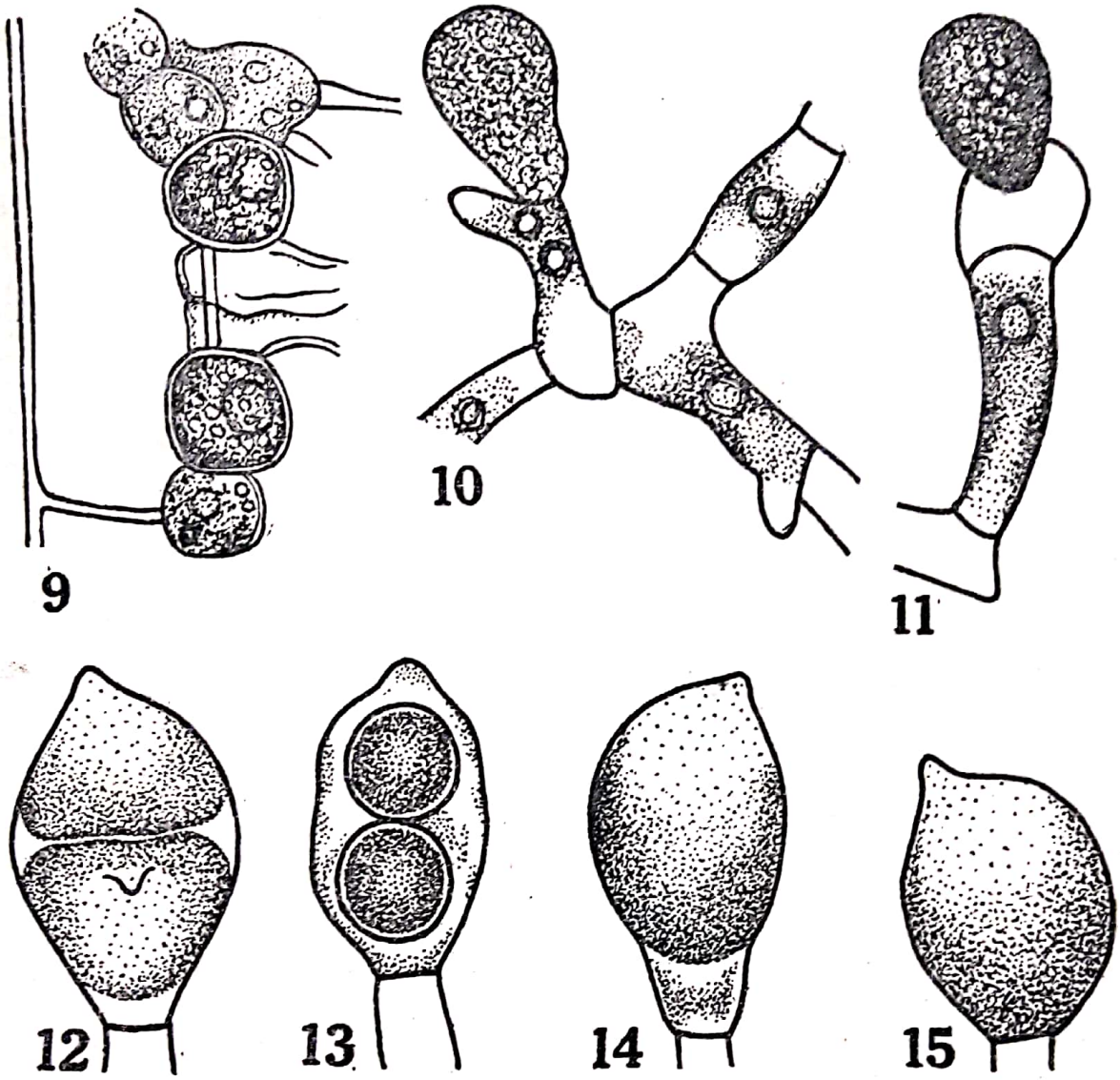

Fig. 9. Oogonia and empty oogonia of *Aphanochaete*. Fig. 10. Oogonium of *Chaetonema* with egg still inside. Fig. 11. Oogonium of *Chaetonema* showing liberation of the egg. Fig. 12. *Awadhiella indica* showing oogonium with two eggs and two beaks. Fig. 13. Oogonium of *Awadhiella indica* with two fertilised eggs (young oospores). Fig. 14. Oogonium of *Awadhiella indica* with one egg and residual cytoplasm. Fig. 15. Oogonium of *Awadhiella indica* with a single egg formed from entire contents and with no residual cytoplasm.

green alga except *Sphaeroplea* (Fritsch, 1946). But, in this respect, *Awadhiella* stands at higher a transitional level, since formation of a single egg per oogonium is also common. It would appear that this genus has not yet come to establish the condition of producing only one egg per oogonium which is characteristic of all oogamous chaetophoralean algae. The second primitive character of *Awadhiella* concerns the degree and extent of utilisation of the oogonial protoplast in the formation of the egg(s). Here also, this genus shows a gradation and range. The most primitive condition is shown by stages where to eggs are organised in each oogonium (Figs. 12 & 13). The next stage, marking comparative advance, occurs when, quite often, the contents of the oogonial cell are not completely used up in the formation of the single oosphere and a small part of the cytoplasm is

excluded from the egg proper (Fig. 14). This enucleate cytoplasm persists as a small, ill-defined mass at the base of the oogonium while the rest of the protoplast organises itself in the form of one or two eggs. These portions of residual cytoplasm are usually compressed to conform to the space available at the base of the oogonial chamber after accommodating the swollen oosphere. They invariably degenerate finally. Such stages indicate progressive sterilisation of the supernumerary eggs or their protoplast. It may be mentioned that *Sphaeroplea* Agardh is the only other oogamous green alga known so far, in which a small amount of sterile residual cytoplasm is left out during oogenesis. It is, however, worth noting that in this feature also, *Awadhiella* shows a gradation. Quite often, oogonia containing a single egg are seen without any trace of residual cytoplasm (Fig. 15). These mark the perfect stage in advanced oogamy where a single egg is organised out of the entire contents of the parent oogonium.

The development of an oogonial beak on the megagametangium seems to have proceeded parallel to the evolution of the oogonium. In *Aphanochaete*, a well-pronounced beak is not formed (Fig. 9) and liberation of the quadriflagellate megagamete occurs by a rupcure of the oogonial wall. This condition is similar to what happens in the genera showing isogamy and anisogamy. In *Chaetonema* also, there is no distinct beak but the immotile macrogamete is liberated through a terminal opening in the oogonium (Fig. 11). Thus, it may be said that the beak has not been acquired or morphologically differentiated in any genus of Chaetophorales which does not possess advanced oogamy. It appears to be a character associated with *in situ* fertilization of the oosphere and is a feature of advanced oogamy only. According to this evolutionary concept, the genus *Awadhiella* is the first chaetophoralean alga which has acquired a distinct beak on the oogonium (Fig. 15). It is interesting to note that, in this genus, the oogonia developing two oospheres within them, possess two beaks (Fig. 12). The oogonial beak may, thus, be looked upon as a feature intimately associated with the compulsions of endogametic fertilization. From this stage, it is tempting to visualise the prolongation of the terminal beak into a trichogyne-like structure characteristic of the pulvinate species of *Coleochaete*, the prostrate species of which have failed to develop the prolongation of the beak.

It is possible to arrange the above-described stages in a progressive series which may depict the course of evolution of oogamy within the Chaetophorales. Whether evolution has actually progressed along the indicated path or not remains a mute question. Fritsch (1935, p. 284) states that "*Chaetonema* and *Aphnochaete* indicate the manner in which oogamy has evolved within the group". *Awadhiella* bridges the gap and provides the link to the climax stage of *Coleochaete*.

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