CYTOLOGY AND LIFE HISTORY OF *BATRACHOSPERMUM MAHABALESHWARENSIS* BALAKRISHNAN et CHAUGULE

M.S. BALAKRISHNAN and B.B. CHAUGULE*

ABSTRACT. – The paper presents an account of the cytology and life history of *Batrachospermum mahabaleshwarensis* from Maharashtra, India. This species belongs to the section «*contorta*»; it appears similar to *B. globosporum* Israelson (section «*Turficola*») in vegerative characters but differs in its spirally twisted carpogonial branch. The gametophytic chromosome number was determined as n = 7. Cytological evidence shows that meiosis does not occur in the fertilized carpogonium and that the carposporophyte is diploid (2n = 14). It has been shown that the *Pseudochantransia* plants produced by carpospore germination are also diploid. Apical cells of these plants undergo meiosis and differentiate into gametophytes; we interpret these as meiosporangia. Stages in the reduction division preceding the formation of the gametophytic cladome have been critically studied. The two steps in meiosis are characterised by an inequal cytokinesis with subsequent degeneration of the smaller cell, so that finally only one meiospore, accompanied by a pair of elimination cells, remains. The meiospore develops in situ, attached to the *Pseudochantransia* and becomes the *Batrachospermum* plant. Thus, *Batrachospermum* also has a triphasic life history with all three phases forming a composite entity (a chimera) as has been demonstrated by MAGNE for the Lemaneaceae.

The genus *Batrachospermum* is one of the most common of the fresh water red algae with worldwise distribution and it is a basic type included in all curricula. Till recently text book accounts treated this as a typical illustration of the so called «haplobiontic» types with reduction division immediately following fertilization apparently based on the classical accounts of KYLIN (1912, 1917).

* Department of Botany, University of Poona, Pune -411007, India.

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MAGNE (1967 a, b) has convincingly disproved this old idea of zygotic meiosis in the Nemalionales (1) and shown that all florideophyceae have diploid carposporophytes. It has also been shown by several workers that for a number of Nemalionales the life history is triphasic and consists of a sequence of gametangial, carposporangial and tetrasporangial phases, all the three of which are morphologically dissimilar, and with the carposporangial phase developing on the same gametangial phase (see: DIXON 1973, as also BOLD and WYNNE 1978, for full citations of literature in this regard).

However, those Nemalionales in which the gametophyte appears to develop directly as a bud from progametophyte (e. g. *Batrachospermum, Lemanea*) still remained a problem till MAGNE (1960, 1967 a, b) demonstrated that in *Lemanea* the *Pseudochantransia* phase is diploid and that reduction division took place in the apical cells of this phase differentiating into the gametophytic *Lemanea* plants. Though he did not actually investigate any species of *Batrachospermum*, MAGNE suggested that development of the gametophyte of *Batrachospermum* could be very similar to what he found in *Lemanea* (see also, FELDMANN, 1978, p. 182). This assumption was based on an intuitive interpretation of SIRODOT's figure of *Batrachospermum crouanianum* (SIRODOT, 1884, pl. 25, fig. 5) which showed two small appendages looking very much like the «cellules éliminatrices» of *Lemanea*. HURDELBRINK and SCHWANTES (1972) showed by Feulgen cytophotometry in an unidentified species of *Batrachospermum* that the nuclei of the cladomes contain half the amount of DNA than those of their *Pseudochantransia* and EIKHORST - HURDELBRINK (1973) illustrated transitional stages in *Pseudochantransia* supposedly meiotic and similar to those of *Lemanea*. The text book by CHAPMAN and CHAPMAN (1973) is the only one that has incorporated these findings and given the correct position as regards the nuclear cycle and life history of *Batrachospermum* (but unfortunately these authors do not cite any references to support this statement). Recently STOSCH and THEIL (1979) have demonstrated production of *Batrachospermum* cladomes directly from the prostrate system of *Pseudochantransia* with formation of «polar bodies» in a manner similar to that in *Lemanea*. It is to be pointed out, however, that so far there is no critical account of the cytological events in *Batrachospermum* similar to what MAGNE has demonstrated for *Lemanea*.

The genus *Batrachospermum* is of common occurrence in Maharashtra and it was felt desirable to undertake a critical study which would furnish the needed cytological proof and help in revising text book accounts of this basic type.

Among the species of *Batrachospermum* collected for study from various parts of Maharashtra (India) was one from Mahabaleshwar which appeared to

(1) The authors have followed FELDMANN (1976) in adopting this ordinal name. Many workers, however, (e. g. CHRISTENSEN, 1962; DIXON, 1973) consider «Nemaliales» to be the correct form.

be new to science (1). Study of early stages indicated that it was rather favourable material for elucidation of gametophyte development, the point at issue. The material was, therefore, brought to Poona and further studies were made in rough laboratory culture. The ensuing account presents the findings of a critical study undertaken with this as the objective.

MATERIAL AND METHODS

The alga grows on rocks in shaded places of both temporary and permanent streams from July (the beginning of the «Monsoon» season) to February. The *Pseudochantransia* plants resulting from carpospore germination are first observable in July. They grow rather fast and reach full development in about three weeks' time. From late July, the gametangial *Batrachospermum* phase with its characteristic morphology becomes apparent and by the first week of August fairly well developed gametophytes can be collected. By the end of August gametophytes attain full development and fructification can be observed. Peak development and fruiting is seen in September. By the middle of October the alga starts disappearing from most localities. However, at one locality (near Bombay point), well developed plants could be collected upto February and even March.

Collections were made on the following dates in 1972: 15/8/72; 29/8/72; 3/9/72; 19/9/72; 1/10/72; 15/10/72; 5/10/72; 19/10/72. From 1973 to 1977, collections were made at regular weekly intervals on Sundays starting on July 1st every year and ending in the latter half of October, coinciding with the end of the monsoon. Subsequent to October, collections were made at monthly intervals up to March.

All these collections were made from two localities in Mahabaleshwar: the Lingmala and Tiger Path Stream near Bombay point. Representative voucher material is preserved in the author's algal collections.

The material was also brought to Poona for further studies which were made with the aid of laboratory cultures. These studies were used to supplement field observations. Cytological studies to back up observations on developmental morphology were made with the help of whole mounts fixed in Acetic alcohol (1:3) and stained in acetocarmine (RAO, 1953) and Aceto-iron-haematoxylinchloral hydrate (WITTMANN, 1965).

OBSERVATIONS AND DISCUSSION

The plants (gametophytes) (Fig. 1) are 2-6.5 cm high, highly mucilaginous and slight olive-green in colour. Ramification is rich and monopodial, the bran-

(1) While it shows some resemblance to *B. globosporum* Israelson (Section *«Turficola»*), this species differs conspicuously in its twisted carpogonial branch, which places it in the section *«Contorta»*. Primarily, on the basis of this difference, it has been described as a new species by the authors in a separate paper (BALAKRISHNAN and CHAUGULE, 1980).

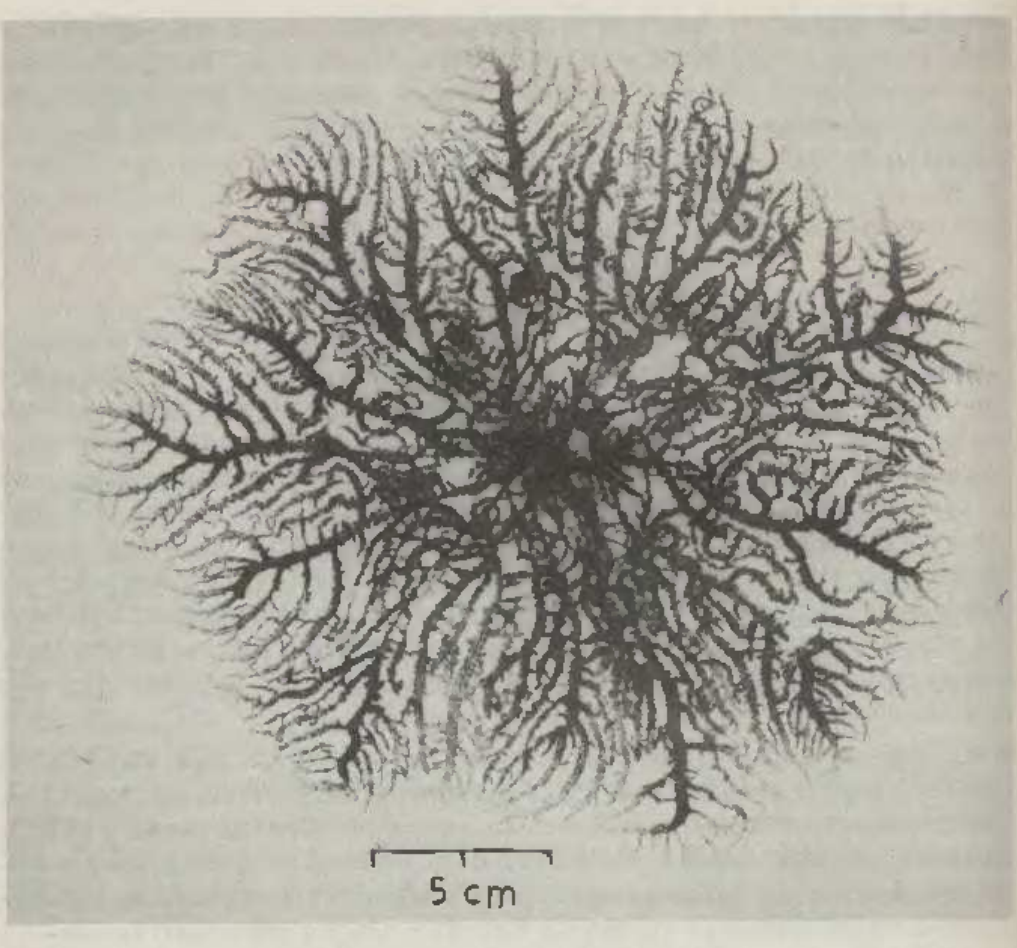

Fig. 1. — *Batrachospermum mahabaleshwarensis* Balakrishnan et Chaugule : general habit.

ches with gradually tapering apices. The axial cells are surmounted by a whorl of globular to ellipsoid basal cells from which arise clusters of determinate laterals (Fig. 2). In old plants the determinate laterals get aggregated into disc-shaped and conspicuous glomeruli. Cells of the primary determinate whorls are uninucleate and more or less uniform subcylindrical; the terminal cells, however, are ellipsoidal. Older portions are corticated, the cortical filaments ultimately enveloping the axial cells completely. Secondary determinate laterals are sparse and short (Fig. 3).

All cells are uninucleate and nuclear division follows the normal mitotic pattern. The small size of the nuclei (1-1.5μm) as also of the chromosomes (fractions of a μm) made critical study of mitosis rather difficult. However, it was possible to ascertain that the haploid gametophytic chromosome number was 7 (Fig. 15-20).

The plants are monoecious. Spermatangia are globular and produced on primary as well as secondary laterals (Fig. 4 et 5). Carpogonial branches always arise from the basal cell and are spirally twisted. The trichogyne is distinctly stalked, conical and compressed (Fig. 6).

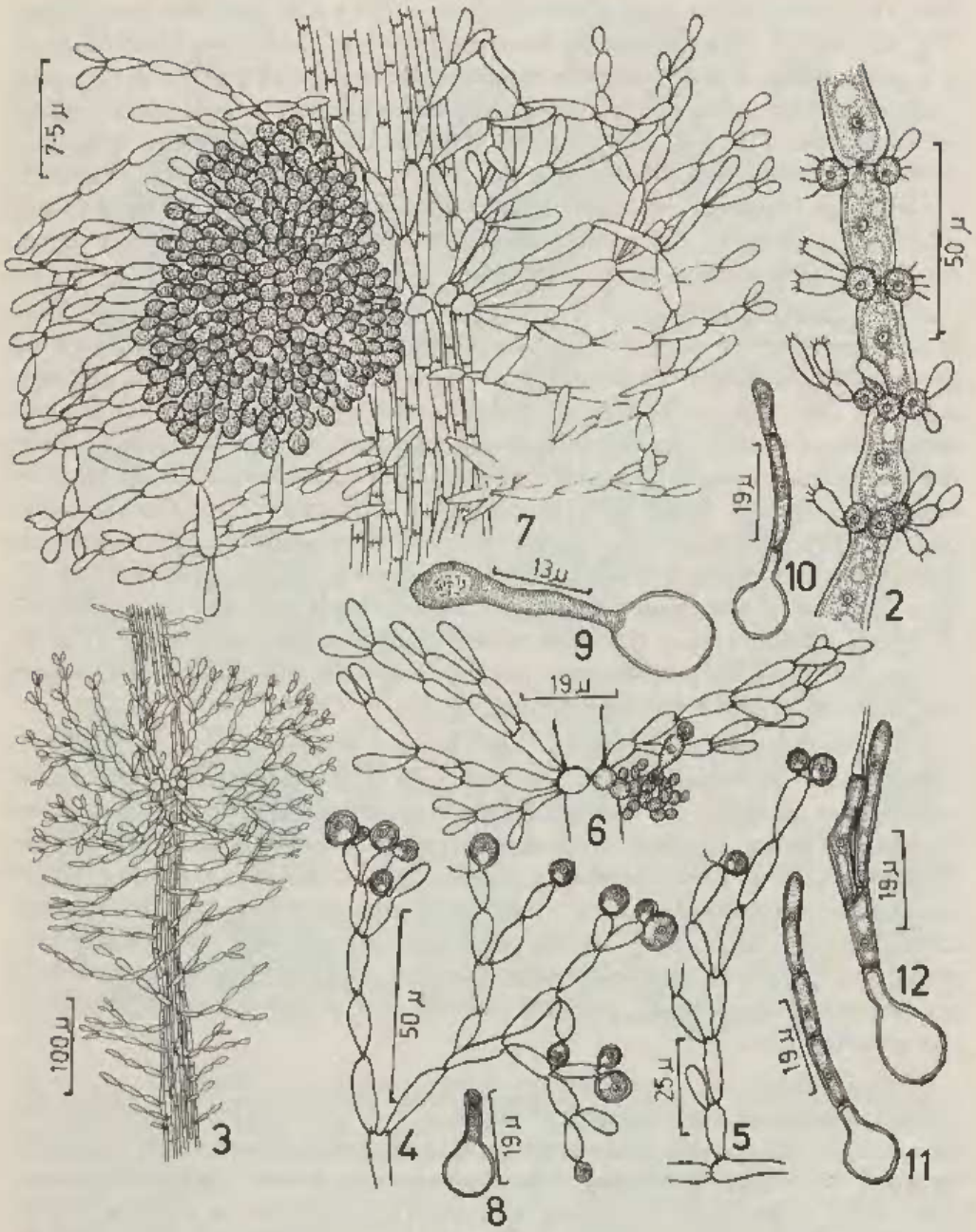

Fig. 2-12. — 2: Young portion of axis showing whorls of basal cells. 3: Portion of old gametophyte showing primary and secondary determinate laterals. 4: Spermatangia on a primary determinate lateral. 5: Spermatangia on a secondary determinate lateral. 6: Twisted carpogonial branch arising from a basal cell. 7: A «node» enlarged to show the primary laterals and axial carposporophyte. 8-12: Stages in carpospore germination.

Our observations on fertilization and carposporophyte development in this species are also in general agreement with those of previous workers. Simultaneously with the division of the zygote nucleus, a lateral protuberance is developed

from the carpogonium. One of the daughter nuclei moves into this protuberance (Fig. 13), which then gets cut off from the carpogonium by a wall and functions as a gonimoblast initial. The other daughter nucleus, which remains in the carpogonium, undergoes further divisions and thus a number of gonimoblast initials are produced (Fig. 14). By repeated divisions of these initials, a subglobose cluster of gonimoblast filaments is ultimately produced (Fig. 7). Cells of the gonimoblast filaments are short, uninucleate and with several plastids. Critical study of mitosis in the gonimoblast filaments clearly showed their diploid nature, revealing a chromosome number of 14 (Fig. 21-25).

The gonimoblast clusters (Fig. 7) are comparatively big, globular, single and inserted on the central axes. Carposporangia are formed terminally on the gonimoblast filaments. Carpospores are produced singly from each carposporangium. The carpospores do not appear to need a resting period prior to germination. Many of them could be observed germinating while still entangled among the determinate laterals of the glomerulus. About 18 hours after settling, a tubular prolongation (germ tube) is produced. The contents of the carpospore pass into the germ tube (Fig. 8) and the carpospore is then separated from the germ tube by a septum. The nucleus in the germ tube then divides mitotically (Fig. 9). One of the resultant daughter nuclei migrates to the tip of the germ tube and simultaneously the germ tube is partitioned by a cross wall (Fig. 10-12). Counts at this mitosis were possible and here the chromosome number was observed to be 14, the diploid number (Fig. 9, 29).

The *Pseudochantransia* plants (Fig. 30) are heterotrichous, the filaments uniseriate and branched, with uninucleate cells. There is a well developed prostrate system consisting of closely adpressed radiating subdichotomous branches. The erect system consists of submonopodially branched uniseriate filaments. The apical cells of erect filaments are generally rounded and a number of them are provided with deciduous unicellular hairs (Fig. 39, 47). Lateral and spherical monosporangia, apparently serving for perpetuation of the *Pseudochantransia* phase, are produced in considerable numbers (Fig. 50-52). After growth of approximately three weeks, terminal cells of erect branches start differentiating into gametophytes.

Critical study of mitosis in the *Pseudochantransia* filaments was rather difficult because of the small size of nuclei (1.7-2.5μm) and small chromosomes. However, it was possible to determine that the chromosome number was approximately $2n = 14$ (Fig. 26-28), as in the germ tubes formed during the germination of carpospores in laboratory cultures (Fig. 29) and in the gonimoblast filaments (Fig. 21-25). This showed that the *Pseudochantransia* phase is diploid, leading to the obvious inference that there has been no reduction division after fertilization. In other words, the carposporophyte is diploid; the carpospores produced by it are also diploid, and these on germination give rise to the diploid *Pseudochantransia* phase.

Apical cells of the *Pseudochantransia* filaments destined to develop into gametophytes enlarge, and become phialide-like (Fig. 31-33). The nucleus enlarges considerably (often reaching 3.5-4μm in diameter) and the cytoplasm takes stain rather intensely. The apical cell then undergoes reduction division.

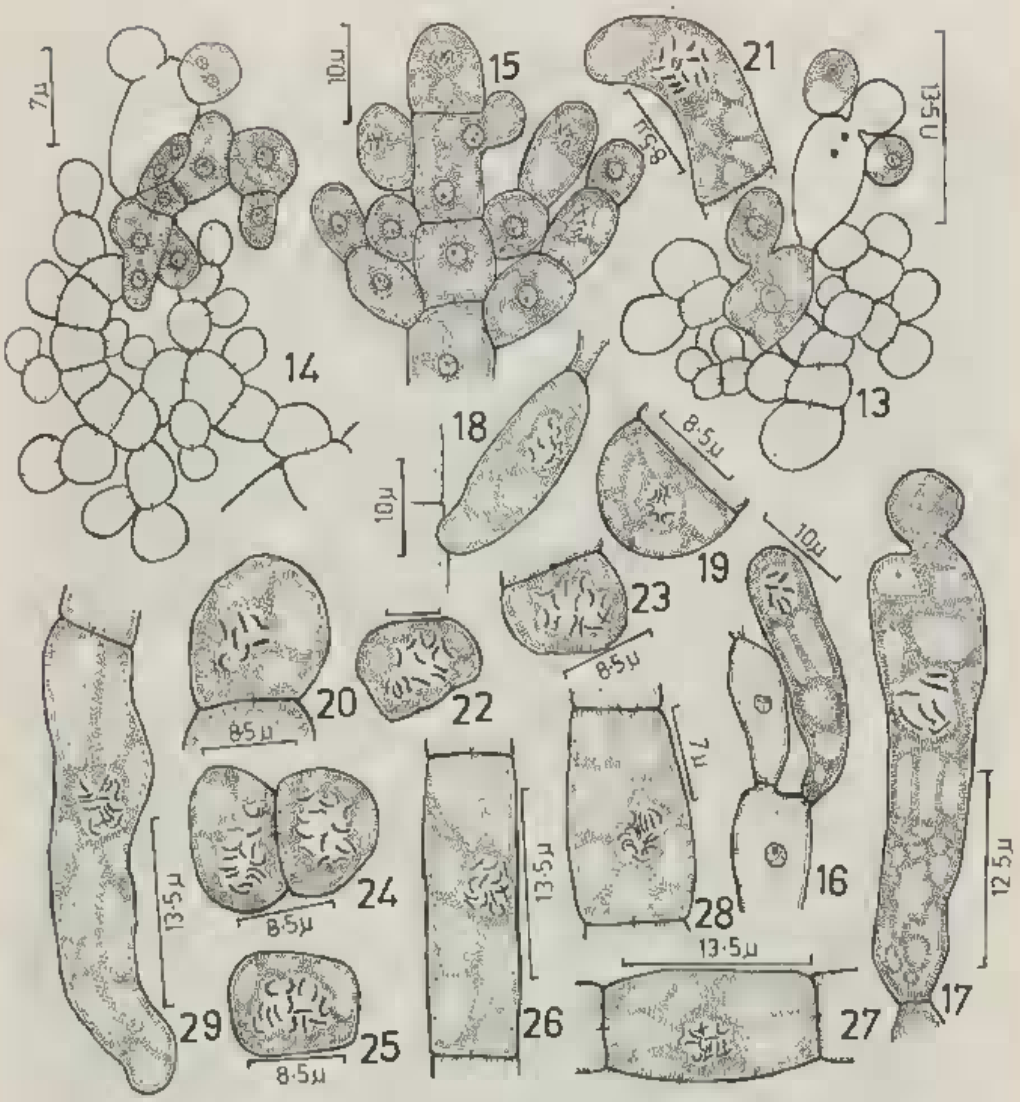

Fig 13-29. — 13: Early post fertilization development showing formation of first gonimoblast initial. 14: Later stage in gonimoblast development. 15: Mitosis in the gametophyte: four of the cells with metaphase showing the haploid number (n = 7) of chromosomes. 16-17: Cells of primary determinate laterals showing the haploid (n = 7) chromosome number. 18. Mitosis in the basal cell of a secondary determinate lateral showing the haploid chromosome number of 7. 19-20: Mitosis in apical cells of the bracteae showing the haploid (n = 7) chromosome number. 21-25: Mitosis in the gonimoblast filaments showing the diploid number (2n = 14) of chromosomes. 26-28: Mitosis in cells of the tetrasporophyte («*Pseudochantransia*») showing the diploid chromosome number of 14. 29: Apical cell of germ filament produced by carpospore germination, showing the diploid chromosome number of 2n = 14.

The earliest stage of Meiosis I seen was a late leptotene (Fig. 34) which was almost zygotene in that evidence of pairing could be faintly discerned at some

points. At pachytene (fig. 35) this was more evident and by this time the chromosomes had also shortened considerably. The single instance of diakinesis observed showed the seven gemini greatly condensed (Fig. 36) and remnants of the nucleolus could still be seen. We were unable to see metaphase I and other later stages of the heterotypic division despite intensive search. The next stage seen is shown in Fig. 37. At this stage, the end of the first (dis-junctional) division, the upper daughter nucleus degenerates, becomes densely pycnotic and is finally extruded witb a small bit of the cytoplasm as a first elimination cell (Fig. 37 left, Fig. 38, arrow). The lower surviving nucleus undergoes the second (homeotypic) division resulting in two daughter nuclei (Fig. 39), of which the upper one degencrates and gets pushed out along with some cytoplasm into a second elimination cell just below the first elimination cell (Fig. 40). This second elimination cell differs markedly from the first not only in the larger amount of cytoplasm included, but also in the nucleus not being so densely pycnotic, often remaining more or less like a normal interphasic nucleus in appearance. The two elimination cells, thus, form a very characteristic tandem. It is interesting to note that MAGNE's figures illustrating the comparable sequence of events occuring in the *Pseudochantransia* phase of *Lemanea mamillosa* (see: MAGNE, 1967 a, Fig. 4) also show this difference between the two elimination cells.

The residual portion, containing the surviving nucleus, enlarges and undergoes a mitotic division (Fig. 40-43) resulting in a diad of cells with the two elimination cells perched on top (Fig. 44). Clear and convincing evidence of reduction having been achieved during the preceeding divisions leading to the formation of elimination cells was also available during this division. Counts at metaphase of this mitosis showed the haploid number of $n = 7$ (Fig. 40), in sharp contrast to the diploid number of $2n = 14$ (Fig. 41 top) in the subtending cells of the *Pseudochantransia*. Of this diad, the lower cell remains more or less unaltered in size and later produces a sparse whorl of determinate laterals. The upper grows out, pushing the elimination cells aside; it then undergoes a series of divisions and develops into the gametophytic plant (Fig. 45-47). The products of this upper cell of the diad soon undergo considerable enlargement (Fig. 47) and develop dense whorls of laterals characteristic of the gametophytic phase whose verticillate organization offers a sharp contrast to the monopodial branching of the subtending *Pseudochantransia* filament (Fig. 48). The elimination cells remain clearly distinguishable throughout development because of their characteristic morphology and pycnotic nuclei (Fig. 37-49, arrows) (see also BALAKRISHNAN and CHAUGULE, 1975; STOSCH and THEIL, 1979).

As a study of figures 44-49 will show, the elimination cells are invariably situated on the suprabasal cell of the gametophyte i. e. the upper cell of the diad which undergoes divisions and develops into the gametophytc. No instance was observed where the elimination cells were present on the basal cell itself. This is so constant a feature that it appears to be of potential diagnostic value.

The observed cytological details of the division (zygotene, diakinesis) (Fig. 34-36) in apical cells of the upright «*Pseudochantransia*» filament show that this is indeed meiotic as suggested by MAGNE (1967b), HURDELBRINK

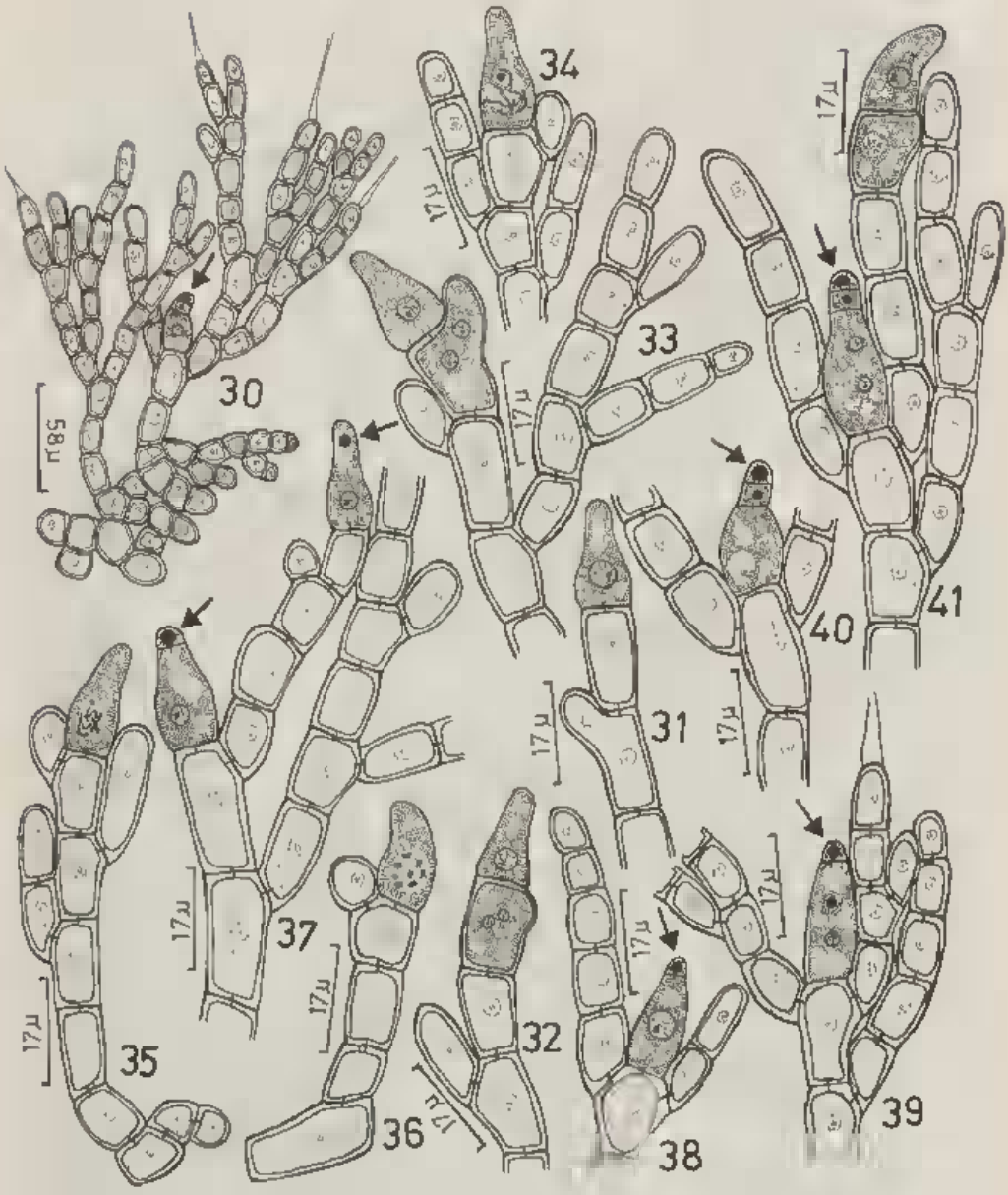

Fig. 30-41. 30: General habit of the tetrasporophytic («*Pseudochantransia*») phase. Arrow indicates differentiation of a gametophyte. 31-33: Stage in the differentiation of the «phialidic» tetrasporangium. 34: Zygotene of Meiosis I in the tetrasporangium. 35: Pachytene of Meiosis I in the tetrasporangium. 36: Diakinesis of Meiosis I in tetrasporangium. 37: End of Meiosis I (upper right, arrow) and formation of first elimination cell (lower left, arrow). 38: A slightly later stage. 39: Telophase of the second division. 40: Metaphase of the first division of the surviving spore prior to gametophyte initiation. Note the reduced chromosome number (n = 7) and the two elimination cells on top (arrow). 41: A still later stage, showing the telophase of the same division. Note the diploid chromosome number (2n = 14) in the dividing cell of the filament at the top.

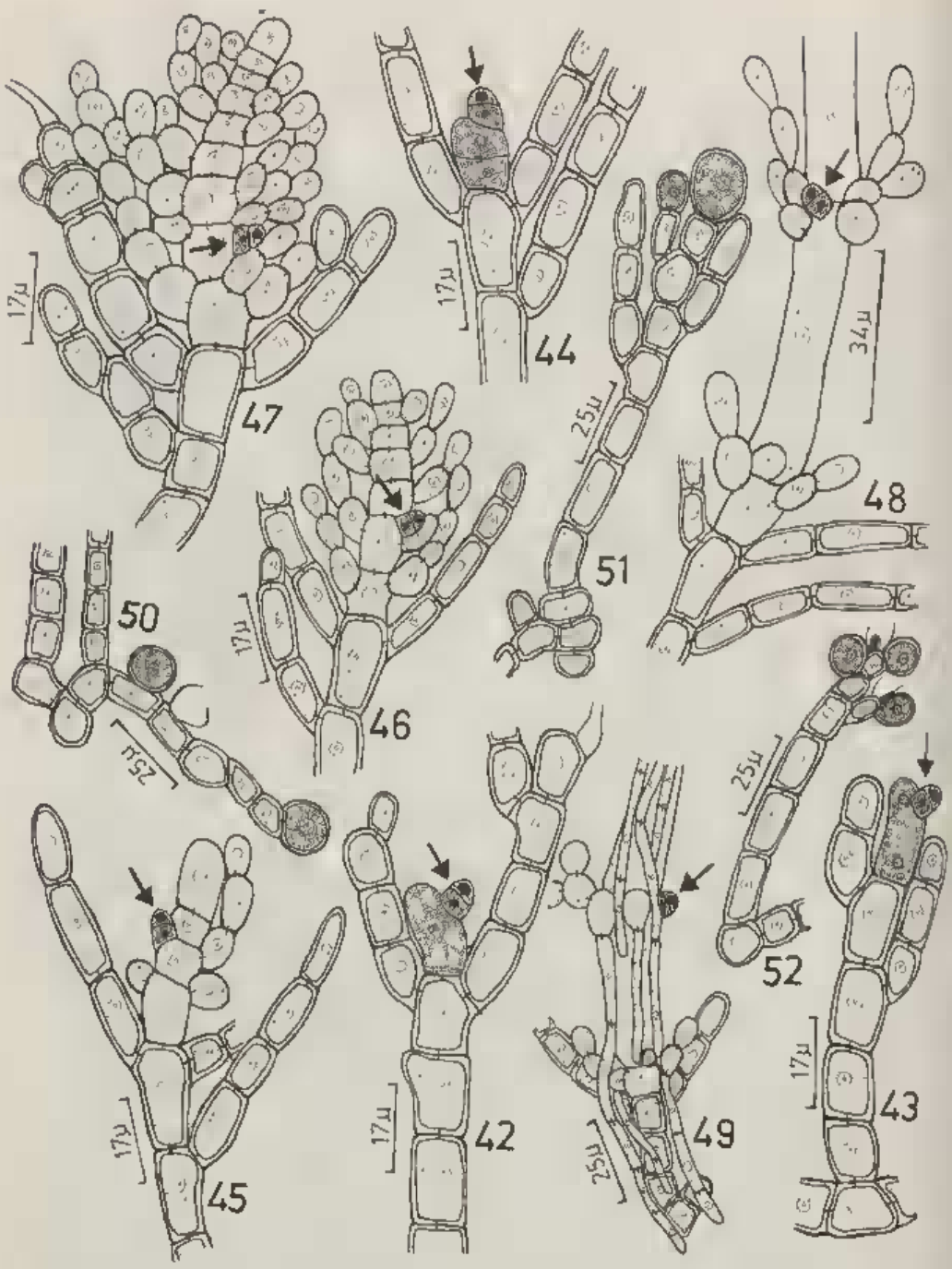

Fig. 42-52. – 42-43: Two stages in the division of the tetraspore initiating gametophyte formation. 44: Completion of the division resulting in a diad. 45-48: Stages in the differentiation and development of the gametophyte. 49: Rhizoidal development at the base of the young, differentiating gametophyte. 50: Monosporangia on a prostrate filament of the tetrasporophyte. 51-52: Monosporangia on the erect filaments of the tetrasporophyte. (In all the figures 42 to 49 the elimination cells are indicated by arrows).

and SCHWANTES (1972), EIKHORST-HURDELBRINK (1973) as also STOSCH and THEIL (1979) on indirect evidence. Moreover, chromosome counts in the cells of the cladomes (haploid, n = 7), carposporophytes (diploid, 2n = 14) and the *Pseudochantransia* phases (diploid, 2n = 14) also provide confirmation of this. The present investigation, therefore, furnishes convincing support to MAGNE's assumption that elimination cells occur in *Batrachospermum* though it was based only on SIRODOT's figure.

While citing MAGNE, DIXON (1973, p. 197) says: «MAGNE (1967 a, b) has claimed that meiosis occurs in the apical cells of the upright filament which produce the gametangial phase. Three of the resulting four nuclei were discarded in small lateral protuberances with one continuing as the origin of the gametangial phase. If correct, this situation represents the first instance in the Rhodophyta of non-sporangial, somatic meiosis». He goes on further to say that the findings of HURDELBRINK and SCHWANTES (1972) «suggest that meiosis in an unidentified species of *Batrachospermum* occurs in a position equivalent to that suggested by MAGNE for *Lemanea*». Echoing DIXON, CHAPMAN and CHAPMAN (1973, p. 272) also say that in the *Pseudochantransia* phase «eventually an apical cell undergoes reduction division, three nuclei abort and the new haploid cell gives rise to a new adult *Batrachospermum* plant». Very recently, STOSCH and THEIL (1979) have reported a similar situation in two forms of *Batrachospermum* which lack a distinct *Pseudochantransia*, the cladomes developing directly from the prostrate crustose growth. But they figure only polar bodies (= the elimination cells of MAGNE) in these two taxa without giving cytological details. They have, however, indicated that in *B. arcuatum*, a species producing the *Pseudochantransia* phase, typically meiotic chromosome morphology has been observed, though they do not give any illustrations.

There are two points which appear to merit further discussion: 1) The implication that four haploid nuclei are produced, and that out of these, three are discarded in small lateral protuberances, the survivor continuing as the gametangial phase, and 2) the concept of non-sporangial or «somatic meiosis».

1) An examination of MAGNE's (1967 b) illustration (Fig. 1-4) clearly shows that only three nuclei are formed, not four. The first division gives rise to two nuclei out of which one (no doubt the equivalent of two haploid spore nuclei though single) degenerates; at the end of second division another out of the pair resulting is also eliminated so that in the process of meiosis two nuclei are extruded and one survives. The extruded nuclei go into the «elimination cells». Thus, though interpretatively the formation of four nuclei can be visualized, actually only three are formed. Two of these do not survive and are eliminated. The survivor (equivalent of one spore) produces the gametangial phase. Commenting on this, MAGNE (1969) himself had earlier said that meiosis, although permitting two successive divisions, of which the first has heterotypic characters, does not result in the production of four haploid cells, but of only one; the relict, after elimination, in two small lateral basal cells, of one of the daughter nuclei of each of the karyokinesis (see also: FELDMANN, 1978, p. 180). A somewhat similar sequence in meiosis has been reported during auxospore formation in some diatoms (GEITLER, 1927 a, b). Our own

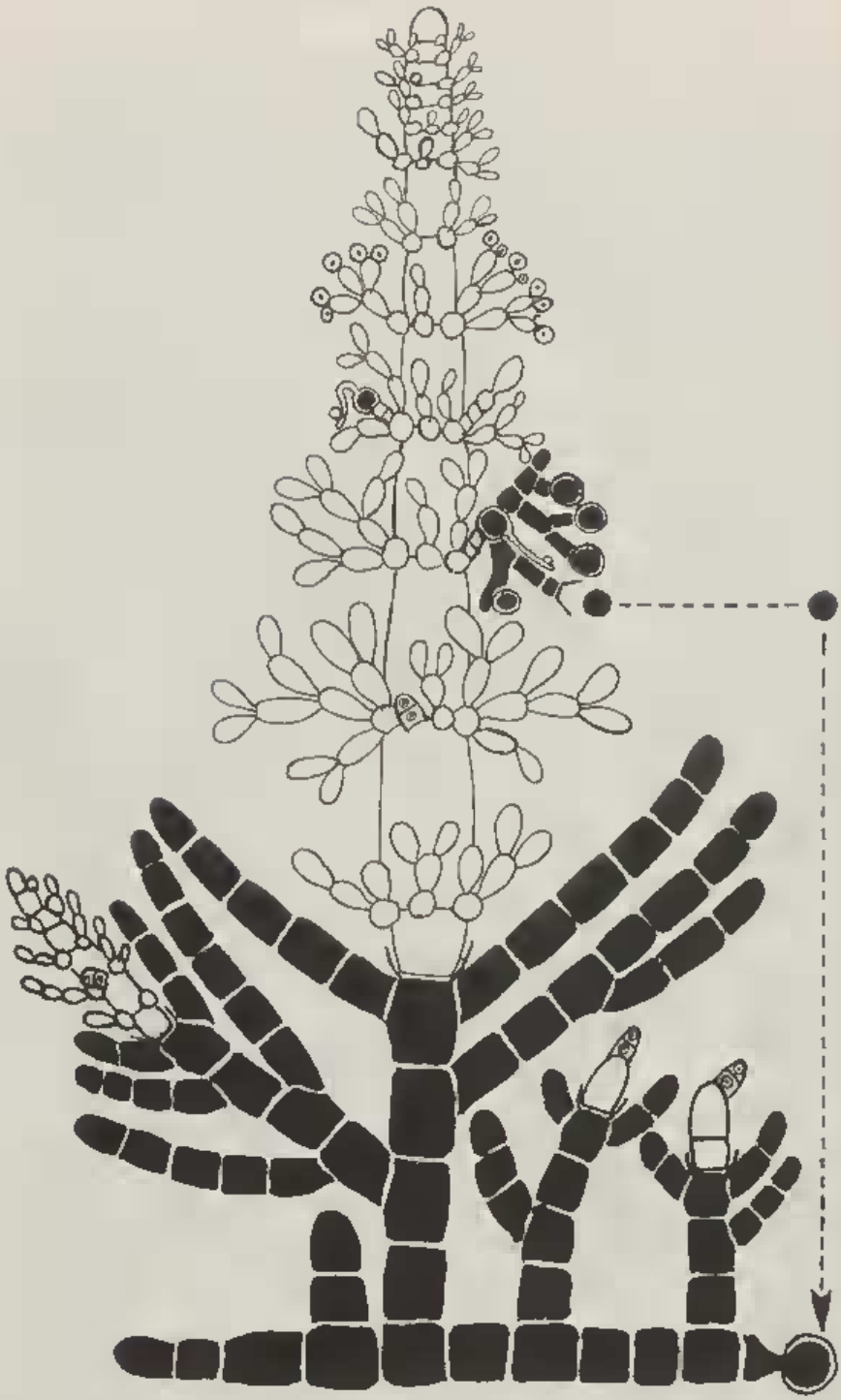

Fig. 53. — Schematic representation of the complete *Batrachospermum* plant to bring out the telescoping of the three phases into a single composite entity. (Solid black indicates diploid constitution).

investigation also clearly shows a sequence exactly like what MAGNE has described for *Lemanea*. The statements of DIXON (1973) as well as CHAPMAN and CHAPMAN (1973) are, therefore, incorrect and have to be amended to fall in line with the correct description as given by MAGNE himself and more recently by STOSCH and THEIL (1979).

2) In his review of life cycles in the Rhodophyceae MAGNE (1972) has discussed instances of the continuity of the tetrasporophytic and gametangial phases which he visualizes as «the implantation of the gametophytes on the tetrasporophyte», citing known instances of «syntagmatic germination» of tetraspores in *Agardhiella tenera* (OSTERHOUT, 1896), *Anatheca montagnei* (BODARD, 1966), etc. MAGNE points out that if this behaviour, which is facultative in the genera mentioned, is established as a permanent feature of the life cycle, a type of development as seen in *Lemanea* (and *Batrachospermum*) can result. The authors are fully in concurrence with this view. In fact, they would go further and say what occurs in *Lemanea* and *Batrachospermum* is not «somatic» meiosis but sporangial meiosis. The «apical» cell of the «*Chantransia*» phase in which it takes place is not a vegetative cell, but a tetrasporangium, the legitimate seat of meiosis, which is undifferentiated and thus indistinguishable from other vegetative cells. Unlike a normal tetrasporangium undergoing successive or simultaneous partition into spores, the contents here remain undivided right up to the end of meiosis. At the end of the heterotypic division one daughter nucleus degenerates and at the end of the homeotypic division another. Similar instances are not unknown. A close parallel is perhaps provided by the «Cryptotetrad» or «Pseudomonad» pollen grains of the Cyperaceae. The extrusion of degenerating nuclei with bits of the protoplast as elimination cells has a rough parallel in the megasporogenesis of angiosperms. In *Lemanea* and *Batrachospermum*, as in the cases above mentioned, germination of spores resulting in the gametophyte is endosporangial and syntagmatic. Hence, the sporangial phase and the gametangial phase are in tandem. To quote MAGNE : «the gametophytic phase is implanted on the tetrasporophyte».

Thus, as in *Lemanea* (MAGNE, 1967 a, b) the Mahabaleshwar *Batrachospermum* also has a triphasic «*Polysiphonia* type» of life cycle, with a haploid gametophyte (the alga) alternating with a diploid carposporophyte and a diploid tetrasporophyte (The *Pseudochantransia*). Only, all these phases are telescoped into one another as a single composite entity (Fig. 53), or as STOSCH and THEIL (1979) have stated, the biont is a chimera composed of the diploid *Pseudochantransia* with the haploid gametophytic cladome «grafted on to it and after fertilization, the diploid carposporophyte grafted on to the cladome». (See also: BALAKRISHNAN, 1977, 1978).

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