
Chapter

12

Vegetative growth and organization

ROY J. COOMANS
MAX H. HOMMERSAND

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I. INTRODUCTION

The red algae have traditionally been divided into two subclasses, the Bangiophycidae and the Florideophycidae, based on differences in vegetative morphology, reproduction, and life histories. Thalli of Florideophycidae are essentially pseudoparenchymatous, consisting of aggregations of filaments that grow almost exclusively through the division of apical cells. As we will show, filamentous growth also prevails in early stages of development in most

Bangiophycidae, although the morphology of the adult thallus is highly variable, ranging from unicellular or colonial to filamentous or parenchymatous. The vegetative morphology of red algae has been described and illustrated by Oltmanns (1922), Fritsch (1945), Kylin (1956), and Dixon (1973). A recent review by Gabrielson and Garbary (1986) brings the literature up to date, with coverage of more recent observations on heterotrichy, the initiation of upright axes, and thallus differentiation.

Several markers of morphogenetic events can be

observed with light microscopy, including wall growth, changes in cell size and shape, changes in the density and distribution of the cytoplasm, internal rearrangements of organelles, nuclear division, and cell division. In this chapter we will describe the major patterns of vegetative growth in Rhodophyta, emphasizing the critical role played by mitosis and cytokinesis. We will focus on primary growth. The formation of secondary tissues is not well documented and will not be covered. The majority of the observations reported here are based on research conducted by the senior author as a part of his Ph.D. dissertation at the University of North Carolina at Chapel Hill (Coomans 1986). Material was preserved in 5% formalin-seawater and stained according to the aceto-iron-hematoxylin-chloral hydrate method of Wittmann (1965), as modified by Coomans (1986), or with aniline blue (Gabrielson & Hommersand 1982a).

Three major patterns of mitosis and cytokinesis were seen that relate to the mode of vegetative growth and level of thallus organization. One of these characterizes the Bangiophycidae. A second type is found in the Acrochaetales, Nemaliales, and Batrachospermales, orders regarded as primitive among the Florideophycidae. The third type predominates in the Bonnemaisoniales, Gelidiales, Gigartinales, Rhodymeniales, and Ceramiales, orders usually considered to be advanced within the Florideophycidae. The Palmariales, Hildenbrandiales, and Corallinales were not studied and will not be discussed. Distinguishing characters include the location and orientation of the mitotic apparatus within the dividing cell, the arrangement of the chromosomes during metaphase and anaphase, the path of migration of the two sets of daughter chromosomes during anaphase, and the timing of septum initiation.

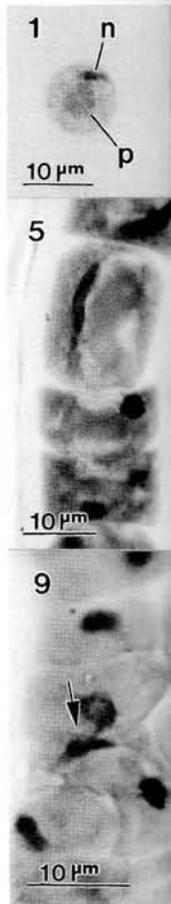
II. BANGIOPHYCIDAE

Light microscope observations of cell division in *Porphyridium* sp. (Porphyridiales) (Figs. 12-1 to 12-4), *Erythrotrichia carnea* (Erythropeltidales) (Figs. 12-5 to 12-8), and *Porphyra carolinensis* (Bangiales) (Figs. 12-9 to 12-12) suggest that a common pattern of mitosis and cytokinesis prevails throughout the Bangiophycidae. Our observations are in good agreement with published descriptions and figures of *Porphyra* (Krishnamurthy 1959; Pringle & Austin 1970; Yabu 1963, 1970), *Bangia* (Yabu 1966), and *Boldia* (Nichols 1964a). The nucleus is elongated immediately prior to and during prophase (Figs. 12-1, 12-5, 12-9). As division proceeds, the chromo-

somes aggregate to form a plate or ring at metaphase within an extended, spindle-shaped nucleus (Fig. 12-6). During anaphase the interzonal spindle elongates greatly, often becoming flexed over the surface of the pyrenoid, when present (Fig. 12-2), and each set of daughter chromosomes is arranged in a partial or complete ring (Figs. 12-7, 12-10). At late anaphase the dividing nucleus can span the entire length or breadth of the cell (Figs. 12-3, 12-11). Cytokinesis takes place after daughter nuclei have formed through annular ingrowth of a broad cleavage furrow (Figs. 12-4, 12-8, 12-12).

Vegetative growth is apical, intercalary, or diffuse (Garbary et al. 1980). Early stages of development following spore germination often show apical growth followed by a shift to intercalary divisions and diffuse growth. *Rhodochaete parvula*, the sole member of the Rhodochaetales, is strictly filamentous. According to Schmitz (1897), vegetative growth takes place exclusively by means of transversely dividing apical cells. The wall of apical cells is thinner and less dense at the tip (Pueschel & Magne 1987), presumably reflecting tip growth. The presence of structurally simple pit plugs has been confirmed with electron microscopy (Pueschel & Magne 1987). Boillot (1975) demonstrated the presence of a sexual alternation of generations in which monospores of the gametophyte and presumed meiospores of the sporophyte undergo bipolar germination, whereas the diploid, sexually produced carpospores and diploid monospores of the sporophyte undergo unipolar germination. The mature thallus consists of pinnately to irregularly branched, uniseriate filaments in both generations.

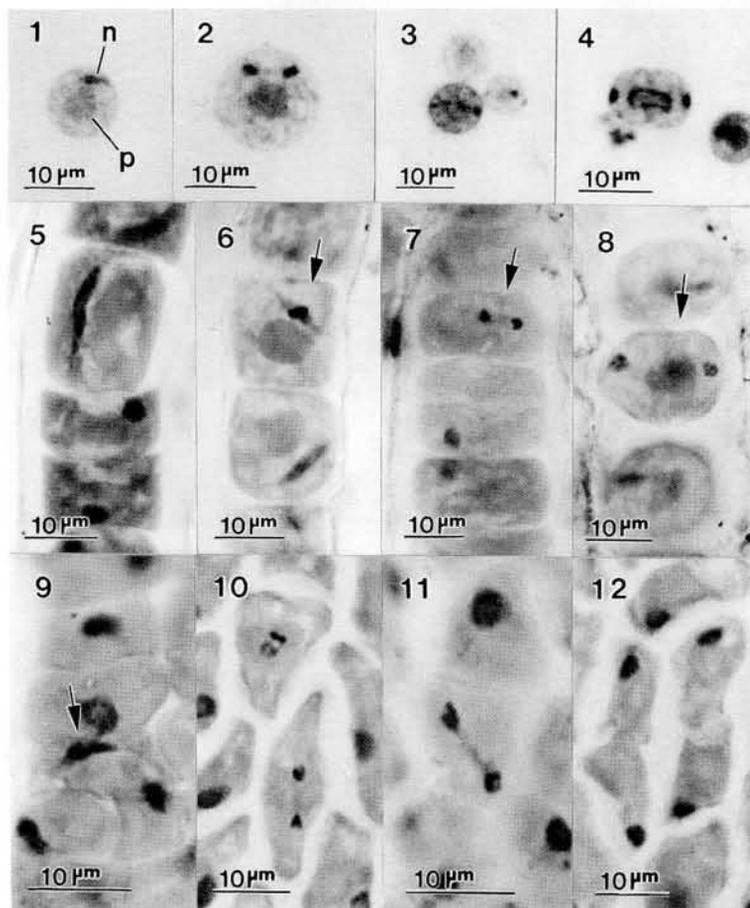
The Porphyridiales contains unicellular and colonial genera; colonial taxa are either amorphous or pseudofilamentous in construction (Garbary et al. 1980). The thallus of *Stylonema alsidii* (formerly *Goniotrichum alsidii*; see Wynne 1985) is composed of uniseriate filaments that branch in a manner resembling the false branching of certain cyanobacteria (Fig. 12-13), but the absence of longitudinal divisions during branch initiation has never been clearly demonstrated. *Stylonema cornu-cervi* and *Goniotrichopsis sublittoralis* are pleuriseriate (Garbary et al. 1980). Isolates of *Chroodactylon* investigated in culture by Lewin and Robertson (1971) (as *Asterocytis*) produced a unicellular form resembling *Chrootheca* when grown in reduced salinity. Gargiulo et al. (1987) found that the thallus of *Erythrocladia irregularis* (Erythropeltidales) converts to an irregular aggregate of unicells when grown under nutrient-enriched conditions and cautioned that some unicellular entities may be incorrectly placed



Figs. 12-1 to 12-4 (Co.). 12-1: Prophase. 12-2: Anaphase. 12-3: Cytokinesis. 12-4: Cytokinesis. Figs. 12-5 to 12-8 (Co.). 12-5: Prophase. 12-6: Anaphase. 12-7: Anaphase. 12-8: Cytokinesis. Figs. 12-9 to 12-12 (Co.). 12-9: Prophase. 12-10: Two cells in late anaphase. 12-11: Cytokinesis. 12-12: Cytokinesis.

in the Porphyridiales (see discussion).

The Erythrocladia crustose, filamentous construction (Garbary 1980) is characteristic of holdfast or a monotypic stage following germination (1968; Howard 1968). Apical in the Erythrocladia intercalary divi-



Figs. 12-1 to 12-4. *Porphyridium* sp. (cultured material, Carolina Biological Supply Co.). 12-1: Prophase; nucleus (n), pyrenoid (p). 12-2: Early anaphase. 12-3: Late anaphase. 12-4: Cytokinesis.

Figs. 12-5 to 12-8. *Erythrotrichia carnea* (North Carolina). 12-5: Extended nucleus at early prophase. 12-6: Metaphase (arrow). 12-7: Anaphase (arrow). 12-8: Cytokinesis; broad cleavage furrow (arrow).

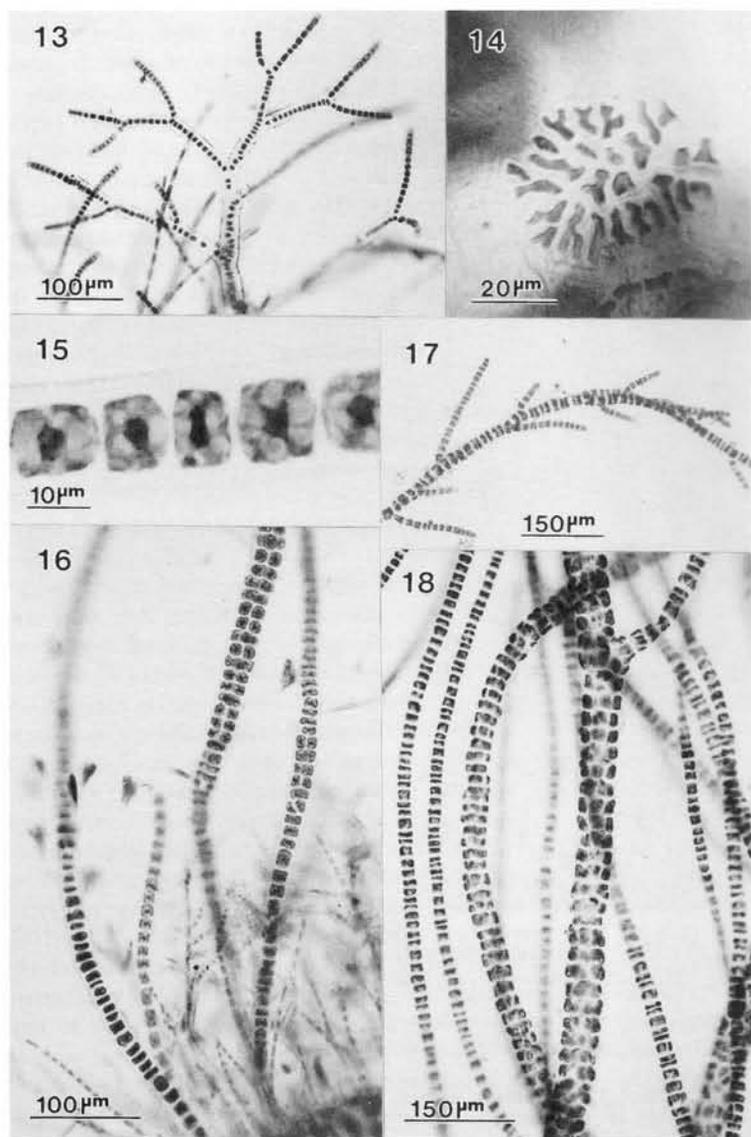
Figs. 12-9 to 12-12. *Porphyra carolinensis* (North Carolina). 12-9: Prophase (arrow). 12-10: Two cells in anaphase; chromosomes form partial or complete rings. 12-11: Late anaphase. 12-12: Two pairs of daughter cells of recent divisions.

in the Porphyridiales (see Chapter 18 for further discussion).

The Erythropeltidales contains species that are crustose, filamentous, saccate, or foliose in construction (Garbary et al. 1980). Germinating spores characteristically produce a prostrate filamentous holdfast or a monostromatic or polystromatic disk. All members appear to go through a filamentous stage following spore germination (Heerebout 1968; Howard & Parker 1980; Hus 1902). Growth is apical in the earliest stages of development, but intercalary divisions soon begin to contribute to the

growth of the thallus. The thallus of *Erythrocladia subintegra* is discoid. Apical cells at the thallus margin become retuse to Y-shaped and divide obliquely in alternating sequence to generate a pseudodichotomous branching pattern (Fig. 12-14). Repeated divisions of intercalary cells generate a raised, saccate region in the central part of the disk (Gargiulo et al. 1987).

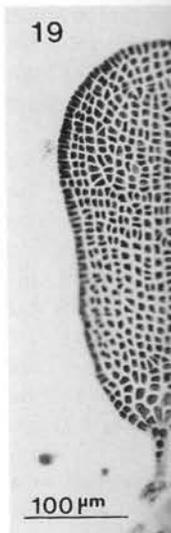
In *Porphyropsis coccinea* monospores germinate into monostromatic disks like those of *Erythrocladia*, but with continued growth vesicles produced from the central area rupture, forming monostromatic



Figs. 12-13 to 12-18. 12-13: *Stylonema alsidii* (North Carolina). False branching. 12-14: *Erythrocladia subintegra* epiphytic on *Polysiphonia* sp. (North Carolina). 12-15, 12-16: *Erythrotrichia carnea* (North Carolina). 12-15: Uniseriate portion showing thick, common wall. 12-16: Filaments becoming multiserial. 12-17, 12-18: *Compsopogon* sp. (cultured material). 12-17: Branch initiation near the apex. 12-18: Uncorticated and corticated filaments.

blades (Garbary et al. 1980; Murray et al. 1972). *Smithora naiadum* first produces a polystromatic basal cushion (Garbary et al. 1980) that gives rise to ovate, monostromatic blades. A filamentous conchocelis-like stage has been reported for both *Porphyropsis* (Murray et al. 1972) and *Smithora* (Richardson & Dixon 1969).

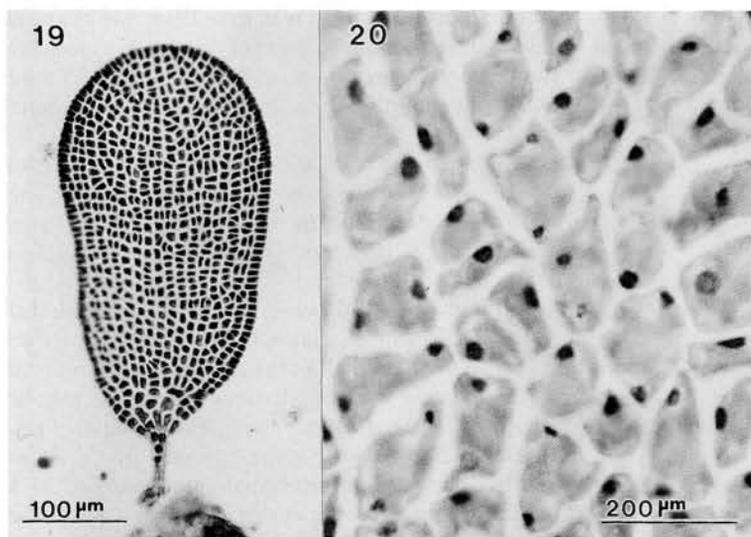
Erythrotrichia carnea possesses an erect, filamentous thallus that may be supported by a small, discoid holdfast. Thalli of *E. carnea* are uniseriate when young but may become pleuriseriate through repeated longitudinal divisions (Figs. 12-15, 12-16). In *E. boryana* longitudinal divisions of cells of the primary filament are restricted to a single plane,



producing a monostromatic thallus (Garbary et al. 1968). *Porphyropsis vexillata* (Garbary et al. 1968). Kornmann (1968) described a heteromorphic, pleiomorphic life cycle of *Porphyrostromium* with a filamentous, uniseriate vegetative phase and a monostromatic, pleiomorphic phase, presumably derived from *Erythrocladia*. The life cycle is thought to characterize the history of a single lineage.

The genus *Compsopogon* is a complex, pleiomorphic genus composed of a number of forms, including uniseriate and pleuriseriate forms with intercalary divisions in the thallus with a distinct holdfast (Garbary et al. 1980).

The *Compsopogon* life cycle is distinct from that of *Erythrotrichia* (Garbary et al. 1980). The life cycle of monostromatic forms of *Compsopogon* may involve a well-developed, pleiomorphic stage produced prior to the formation of a calary division (Krishnamurthy et al. 1980). Behind the calary division, the filament and the thallus are uniseriate (Figs. 12-17). Behind the calary division, the longitudinal divisions of cells (Fig. 12-18; Krishnamurthy et al. 1980) have ceased and the cells have divided several times their original length.



Figs. 12-19, 12-20. *Porphyra carolinensis* (North Carolina). 12-19: Young blade with margin of large, dividing cells. 12-20: Interior of thallus, cells dividing in various planes.

producing a monostromatic blade (Heerebout 1968). *Porphyropsis vexillaris* develops similarly (Heerebout 1968). Kornmann (1984, 1987) has described a heteromorphic sexual life cycle in two species of *Porphyrostromium* that includes a haploid, filamentous phase resembling *Erythrotrichia* and a presumably diploid crustose phase resembling *Erythrocladia*. Thus, both morphological types that characterize the Erythropeltidales occur in the life history of a single species.

The genus *Boldia* (Boldiaceae) possesses a complex, pleiomorphic life history that includes stages composed of a monostromatic disk, apically growing uniseriate filaments, erect and prostrate filaments with intercalary growth, and an erect saccate thallus with diffuse growth (Howard & Parker 1980).

The Compsopogonales is treated as an order distinct from the Erythropeltidales by Gabrielson & Garbary (1986). In *Compsopogon* germination of monospores is bipolar. Rhizoidal and erect filaments may arise directly (Nichols 1964b), or a well-developed rhizoidal holdfast may be produced prior to the initiation of one or more uprights (Krishnamurthy 1962). Both apical and intercalary divisions increase the length of the primary filament and any lateral branches present (Fig. 12-17). Behind the apex, cells undergo oblique longitudinal divisions to produce an irregular cortex (Fig. 12-18; Krishnamurthy 1962). Axial cells that have ceased dividing enlarge, reaching several times their original dimensions at maturity. In

Compsopogonopsis rhizoids are produced by axial cells of the primary filament (*C. leptocladis*, Seto 1982; *C. fruticosa*, Seto 1987) or by the primary cortical cells (*C. japonica*, Seto 1982). A primitive type of pit plug has been described in *Compsopogon* (Chapter 2).

The Bangiales has a heteromorphic life history. The dominant gametophyte is filamentous or foliose and exhibits diffuse growth. The thallus of *Bangia atropurpurea* (reported as *B. fuscopurpurea*) is initially an upright, uniseriate filament with a rhizoidal holdfast. Apical and intercalary divisions increase the length of the filament (Sommerfeld & Nichols 1970). The thallus becomes pleuriseriate through oblique and longitudinal divisions (Drew 1952; Sommerfeld & Nichols 1970), and normally remains unbranched. Germlings of *Porphyra* are also initially filamentous but become foliose through longitudinal divisions of both apical and intercalary cells, beginning at an early stage of thallus development (Rosenvinge 1909). In very young blades there may be an obvious marginal meristem (Fig. 12-19). Subsequent expansion of the blade occurs through diffuse growth, the orientation of cell divisions being variable (Fig. 12-20). Species are either monostromatic or distromatic (Garbary et al. 1980). The sporophytic (conchocelis) stage in Bangiales is filamentous, and cells are joined by pit connections with simple plugs (Cole & Conway 1975; Chapter 2). Spore germination is unipolar and is accompanied by a change in plastid morphology (Pueschel & Cole 1985) and a shift from the production of

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xylan to cellulose in the cell walls (Gretz et al. 1980; Mukai et al. 1981). Early growth appears to result from apical cell divisions (Cole & Conway 1980), but cytological confirmation is needed.

III. LOWER FLORIDEOPHYCIDAE: ACROCHAETIALES, NEMALIALES, AND BATRACHOSPERMALES

As Fritsch (1945, p. 450) pointed out, the most primitive vegetative structures among Florideophycidae are found in members of the *Acrochaetium* complex, now placed in the Acrochaetiales (Garbary & Gabrielson 1987). Branching patterns are simple and there is little differentiation between vegetative cells, even in heterotrichous species. Though the Nemaliales and Batrachospermales possess more complex morphologies, a survey of their life histories reveals the presence of acrochaetoid thalli in both the tetrasporophyte generation and the protonemal stage of the gametophyte generation (West & Hommersand 1981). These three orders also possess pit plugs with two cap layers, a feature otherwise known only in the Palmariales (Chapter 2).

Acrochaetiales and Nemaliales exhibit a common mode of mitosis and cytokinesis, in which nuclear division does not ordinarily take place at the site of future septum formation, but rather basal to it, and the orientation of the mitotic apparatus is variable. The same nuclear behavior is seen in the whorled determinate lateral filaments of *Batrachospermum boryanum* and the pseudochantransia stage of *Lemanea australis* (Batrachospermales).

A. Acrochaetiales

Whereas most recent authors have followed Garbary (1979a) and Woelkerling (1983) in recognizing a single genus, *Audouinella*, in the Acrochaetiales, Stegenga (1979, 1985) distinguishes some five to seven genera based on combinations of chloroplast type, spore germination pattern, and life history characters (see Chapter 18). Spore germination may be unipolar, bipolar, or septate, and thalli may have a unicellular base, a multicellular base, or a heterotrichous habit consisting of filamentous prostrate and erect systems. Gametophyte and sporophyte generations may be heteromorphic and often have distinctly different germination patterns and basal systems (Stegenga 1979, 1985).

Strictly apical deposition of new wall material has been demonstrated in *Audouinella hermannii* by Hymes and Cole (1983) using calcofluor white. Garbary (1979b), working with five species of *Audo-*

uinella, found that most wall growth occurs in apical cells. Subterminal cells were at or near their mature dimensions when cut off, and all cells reached their maximum length when only a few cells behind the apex.

In *Acrochaetium secundatum* from South Africa (Stegenga 1985) spore germination is septate, the prostrate system forming a pseudoparenchymatous disk (Fig. 12-21). Branching of erect filaments is characteristically secund (Fig. 12-22). Nuclear division is initiated following extension of the apical cell or formation of a lateral bud. Nuclear division occurs in the basal half of the dividing cell, proximal to the ensuing septum. Orientation of the mitotic apparatus is variable but most often oblique (Figs. 12-23, 12-24). As is frequently seen in the Bangiophycidae, the chromosomes are arranged in a partial or complete ring at metaphase and anaphase (Figs. 12-25 to 12-27). There are two distinct stages to anaphase migration. The first involves the separation of daughter chromosomes. At its completion one set has come to lie against the side wall; the other set has moved to the opposite side wall or come to lie against the basal crosswall. During migration the two sets of daughter chromosomes frequently twist with respect to one another, rather than moving perpendicular to the plane of the preceding metaphase plate (Fig. 12-28). In the second stage of anaphase the more distal set of daughter chromosomes migrates into the apex of the dividing cell (Fig. 12-29). Nuclear divisions associated with the formation of a lateral initial take place within the parent cell, not in close association with the lateral bud (Fig. 12-30). In *Audouinella violacea*, as in many Acrochaetiales, there is a precocious initiation of the septum prior to the onset of mitosis or during its early stages (Figs. 12-31 to 12-33).

Vegetative cells of most species remain uninucleate due to an absence of cell fusions, secondary pit connections, and nuclear divisions without ensuing cell divisions. Exceptions are the lateral fusions between cells of the pseudoparenchymatous basal system in *Audouinella spetsbergensis* (Dixon & Irvine 1977; Garbary et al. 1982) and *A. concrescens* (West 1970).

B. Nemaliales

Excluding *Galaxaura*, which has an isomorphic alternation of generations, the Nemaliales possesses a heteromorphic life history in which the dominant gametophyte is multiaxial and the tetrasporophyte resembles *Acrochaetium* (West & Hommersand 1981). Germinating tetraspores give rise to a mono-

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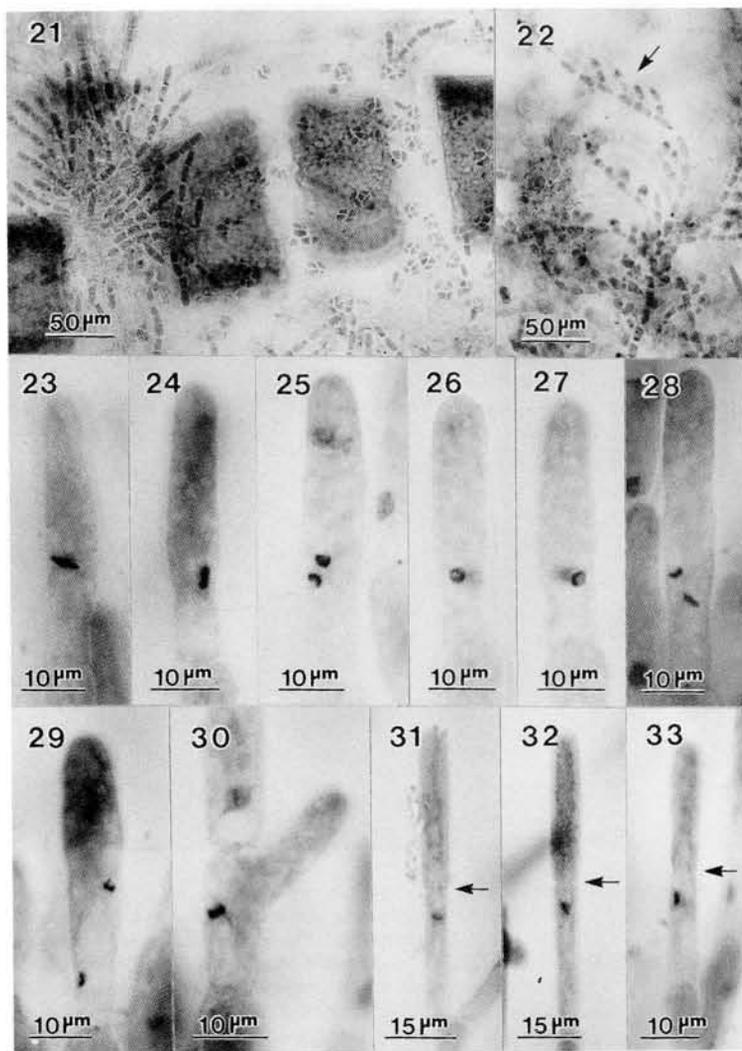
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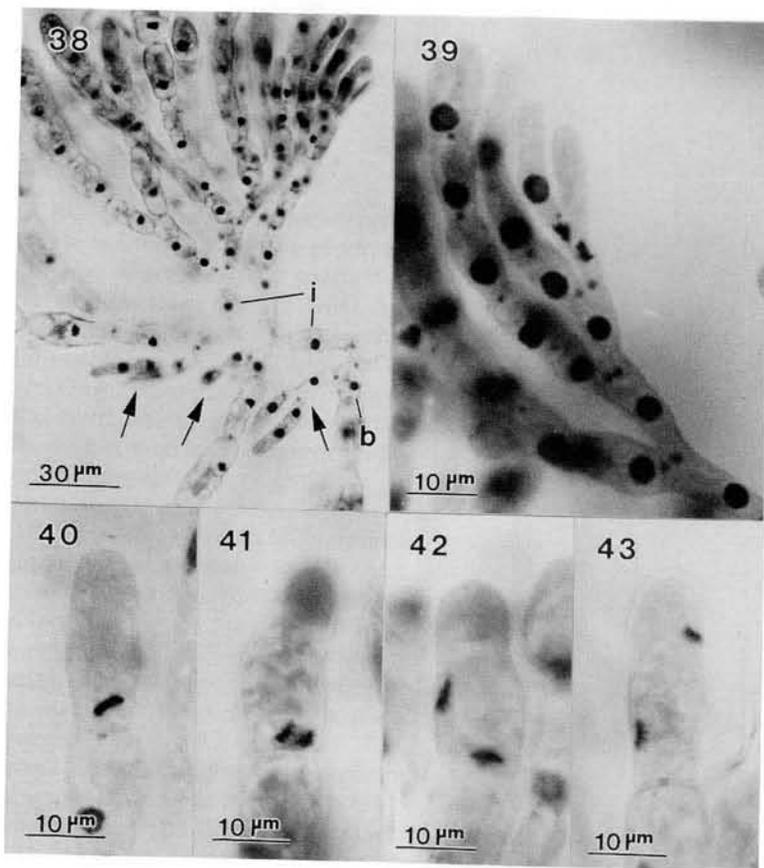


Figs. 12-21 to 12-30. *Acrochaetium secundatum* (South Africa). 12-21: Numerous sporelings epiphytic on *Chaetomorpha linum*. 12-22: Secund branching. 12-23, 12-24: Variation in metaphase orientation. 12-25: Early anaphase. Oblique division; daughter chromosomes form partial rings. 12-26, 12-27: Two focal planes of a cell at the end of the first stage of anaphase migration. Chromosomes form rings and have migrated to opposite sidewalls. 12-28: Anaphase; daughter chromosomes twisting with respect to one another. 12-29: Late anaphase; distal set of daughter chromosomes migrating apically. 12-30: Metaphase; division to form a lateral initial. Figs. 12-31 to 12-33. *Audouinella violacea* (North Carolina). Variation in orientation of metaphase plate. Division located just proximal to precocious septum (arrows).

siphonous protonemal stage. Uprights produced by the protonemal stage may initially be uniaxial or multiaxial.

Little has been added to our knowledge of apical organization in Nemaliales since Oltmanns (1904) introduced the term *Springbrunnentypus* for taxa in

which growth is maintained by a cluster of apical initials. *Liagora mucosa* is representative of the multiaxial habit in Nemaliales (Fig. 12-34). In *L. mucosa* growth results from the activity of five to ten indeterminate filaments, each of which develops sympodially. Apical cells of indeterminate

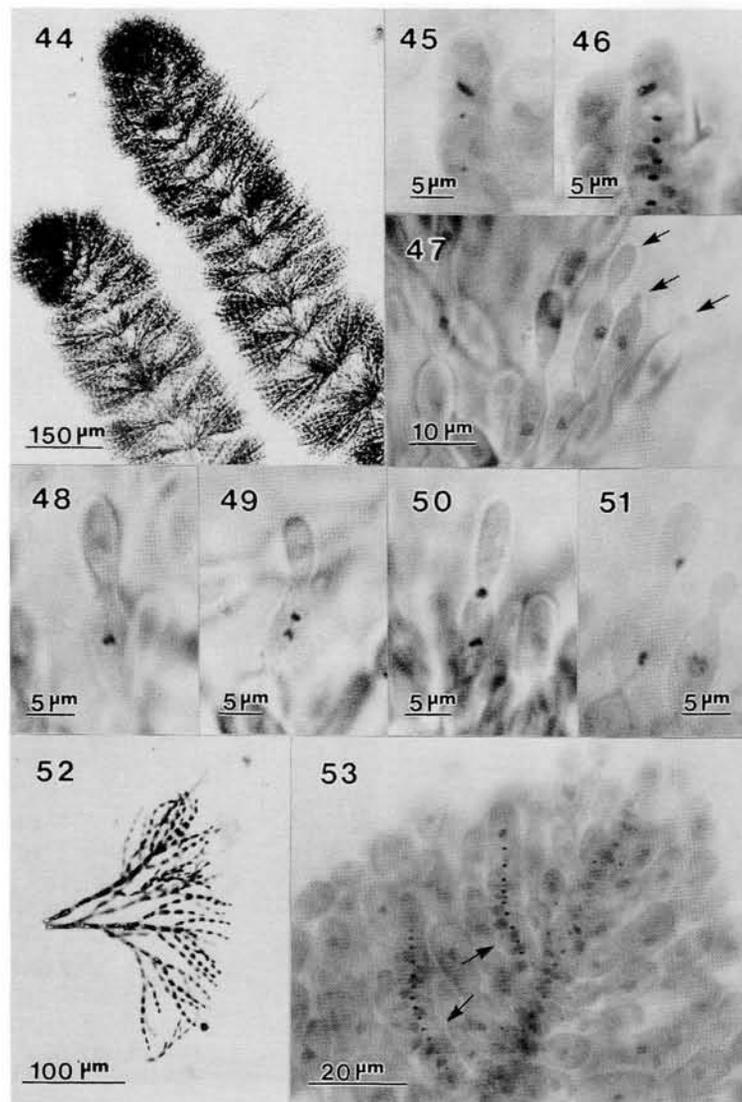


Figs. 12-38 to 12-43. *Liagora mucosa* (Florida). 12-38: Young indeterminate lateral filaments (arrows) arising from two adjacent indeterminate axial filaments (*i*); each is borne on the basal cell (*b*) of a determinate lateral filament. 12-39: Mitosis in subapical cell of indeterminate filament, end of first stage of anaphase migration. Lateral initial will assume the apex. 12-40: Metaphase; determinate filament. 12-41: Early anaphase, determinate filament. 12-42: End of first stage of anaphase migration, determinate filament. 12-43: Second stage of anaphase, distal set of daughter chromosomes migrating into apex.

Liagora has been termed cellulosympodial by Norris et al. (1984). Cellulosympodial growth of indeterminate filaments is not unique to *Liagora mucosa*. Our preliminary observations have verified its presence in *L. farinosa* and *Helminthora australis*. Careful scrutiny of the literature supports the likelihood that cellulosympodial development of axial filaments is a common feature among Nemaliales. Cleland's illustration (1919, text Fig. 1) of the apex of *Nemalion helminthoides* (as *N. multifidum*), Desikachary's drawings of axial filaments of *Helminthocladia australis* (1957, Fig. 15), *Cumagloia andersonii* (1962, Fig. 1), and *Dermonea frappieri* (1962, Fig. 31), Svedelius' illustration of the apex of *Galaxaura diesingiana* (1942, Fig. 6b), and Kjellman's depiction

of an indeterminate axial filament of *Galaxaura falcata* (1900, Pl. 11, Fig. 13) could all be interpreted as illustrating cellulosympodial development.

It is commonly assumed that branching of the thallus in Nemaliales takes place by "periodical separation of the apical threads into two groups" (Fritsch 1945, p. 469). This is not true of *Liagora mucosa*, where indeterminate initials cut off from the basal cell of determinate lateral filaments are responsible for branching. One to two indeterminate filaments are initiated from the basal cell of a determinate lateral filament following the production of its normal complement of two to three determinate filaments (Fig. 12-38). Indeterminate initials are cut off from the determinate filaments of two to four



Figs. 12-44 to 12-53. *Batrachospermum boryanum* (North Carolina). 12-44: Axes with whorled determinate lateral filaments. 12-45: Tilted metaphase plate in apical cell of indeterminate filament. 12-46: Early anaphase in apical cell of indeterminate filament. 12-47: Buds (arrows) forming on apical cells of determinate filaments. 12-48: Early anaphase in apical cell of a determinate filament. 12-49: Midanaphase, determinate filament. One set of daughter chromosomes forms a partial ring. 12-50: Anaphase, determinate filament. Distal set of daughter chromosomes moving into bud through its constricted base. 12-51: Late anaphase, determinate filament. 12-52: Mature determinate lateral filament (basal cell not present). 12-53: Axial filament bearing two abaxial indeterminate lateral filaments (arrows).

adjacent axial filaments over a length of two to four axial segments. The filaments they initiate coalesce to form the axis of a lateral branch. At times the thallus of *L. mucosa* appears to branch at the apex

through a splitting of the indeterminate filaments that compose an axis, but this occurs infrequently.

Nuclear divisions in *Liagora mucosa* take place near the base of a dividing cell in both indeter-

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minate and determinate filaments (Figs. 12-39 to 12-43). The pattern of chromosome migration during anaphase is the same as was described for *Arochaetium secundatum*.

C. Batrachospermales

In the characteristic batrachospermalean life history a macroscopic gametophyte alternates with a diminutive acrochaetoid sporophyte, the pseudochantransia stage (Sheath 1984). The gametophyte of *Batrachospermum* is uniaxial. It consists of branched indeterminate axes, each segment of which bears a whorl of determinate lateral filaments (Fig. 12-44). Indeterminate axes and determinate filaments are distinct in their morphology, cytology, and developmental potentials (Aghajanian & Hommsand 1980).

The apical cell of an indeterminate filament is a domed cylinder that cuts off short, discoid segments basally. In *Batrachospermum sirodotii* apical cells extend by means of tip growth (Aghajanian & Hommsand 1980). In *B. boryanum* nuclear division takes place at or near the site of subsequent septum formation and the metaphase plate is tilted with respect to the cell's axis (Figs. 12-45, 12-46). The basal set of daughter chromosomes appears to migrate to the side of the incipient subapical segment from which the first periaxial cell will be cut off; however, a regular pattern in the arrangement of first periaxial cells on successive axial segments has not been found. With the completion of anaphase migration, daughter nuclei form, a vacuole enlarges between them, and a septum cuts off the new segment.

Periaxial cells are initiated several segments behind the apex as protrusions that extend laterally and curve apically before being cut off by a transverse septum (Aghajanian & Hommsand 1980). The number of periaxial cells per segment varies among species but is most often between four and six (Mori 1975). We have been unable to find a pattern in the sequence of initiation of periaxial cells on an axial segment in *Batrachospermum boryanum*. Each periaxial cell gives rise to a system of branched, determinate filaments. Growth of determinate filaments takes place by budding of apical and subapical cells (Fig. 12-47). Nuclear divisions in determinate filaments of *B. boryanum* resemble divisions in the Acrochaetiales and Nematiales. Mitosis takes place within the body of the parent cell. The exact location and orientation of division is variable; most often, the metaphase plate is oriented obliquely

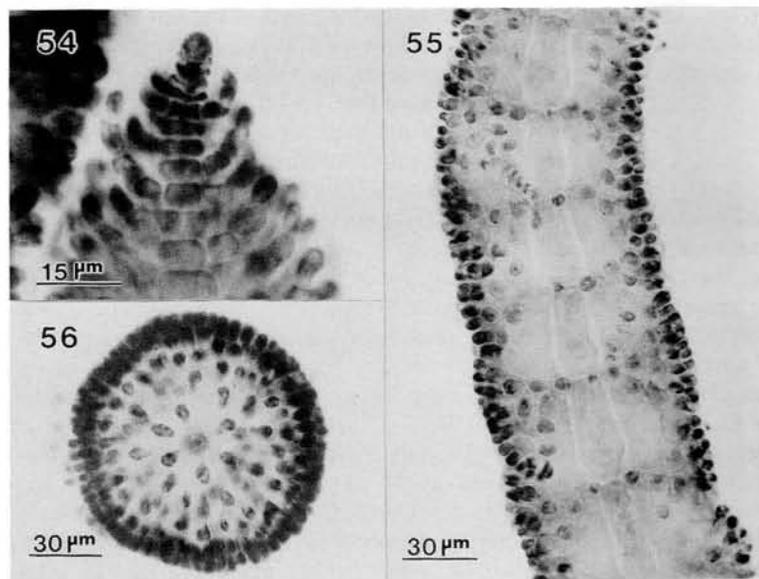
with respect to the long axis of the cell (Fig. 12-48). As daughter chromosomes separate at anaphase, each set is frequently seen to be arranged in a partial or complete ring (Fig. 12-49). After the two sets of chromosomes are well separated, the more apical set moves into the bud through its constricted base (Figs. 12-50, 12-51). This is contrary to the report that in *B. sirodotii* the nucleus migrates from the parent cell into the bud, where it divides, followed by migration of one of the daughter nuclei back into the parent cell (Aghajanian & Hommsand 1980). Branching of determinate filaments is either trichotomous or dichotomous, with the formation of up to six or more orders of branches in *B. boryanum* (Fig. 12-52).

Periaxial cells initiate descending rhizoidal filaments proximally, from their lower side, after the determinate lateral filament is well developed. Descending rhizoidal filaments of successive segments may overlap, enveloping the axis (Sirodot 1884), and can give rise to secondary determinate lateral filaments (Entwistle & Kraft 1984; Israelson 1942).

Indeterminate lateral branches are produced at irregular intervals along the length of an axis. In *Batrachospermum boryanum* an initial is cut off from the distal end of a periaxial cell and rapidly grows to a length of 15-30 segments (Fig. 12-53). Many indeterminate laterals will cease growth at this stage or at a slightly later stage, when periaxial cells and immature determinate lateral filaments have been produced along the base of the indeterminate branch. Others continue to grow, becoming identical to the parent axis. No more than one indeterminate lateral is produced per axial segment, and many segments have none. Though there is no discernible pattern to the arrangement of indeterminate laterals along the length of an axis in *B. boryanum*, axes tend to have a greater number of more fully developed branches on their abaxial surface (Fig. 12-53).

Wall growth has been investigated in *Batrachospermum sirodotii* (Aghajanian & Hommsand 1980). Apical cells of indeterminate filaments, periaxial cell initials, and buds associated with the growth of determinate lateral filaments all show tip growth. Maturing axial cells elongate through the deposition of new wall material in a basal band, whereas intercalary cells of determinate filaments show bipolar band growth.

Apical development and morphology of *Tuomeya americana* is similar to that of *Batrachospermum* (Fig. 12-54), but the determinate lateral filaments are



Figs. 12-54 to 12-56. *Tuomeya americana* (North Carolina). 12-54: Apex. 12-55: Median longitudinal section. 12-56: Cross section; axial cell bearing six periaxial cells.

more compactly arranged. *Tuomeya* possesses a confluent cortex at the surface of the thallus that is separated from the axial filament by a space resulting from the elongation of periaxial cells and the loose arrangement of inner cells of the determinate filaments (Figs. 12-55, 12-56).

The gametophyte of *Lemanea australis* is cylindrical and tapers gently toward the apex. Growth is uniaxial. The apical cell of an indeterminate filament cuts off short discoid segments basally (Fig. 12-57). Behind the apex, axial cells expand centrifugally. Each undergoes successive periclinal divisions to cut off four periaxial cells in an ordered sequence, with the second opposite the first and the fourth opposite the third. The first periaxial cells on successive axial segments are arranged in a 60-degree spiral.

Development of the cortex from periaxial cells occurs through a similar process of cell expansion and cleavage, and follows a regular pattern of cell divisions. First and second periaxial cells undergo a slightly different series of divisions than the third and fourth (Atkinson 1890; Sirodot 1872). Cortical development in *Lemanea australis* has been described in detail by Mullahy (1952). First and second periaxial cells cut off two initials of ascending filaments, one of which divides to give a third ascending filament, two initials of descending filaments, and a ray cell. Third and fourth periaxial cells each initiate a single ascending filament and two descending filaments. Initials of ascending and

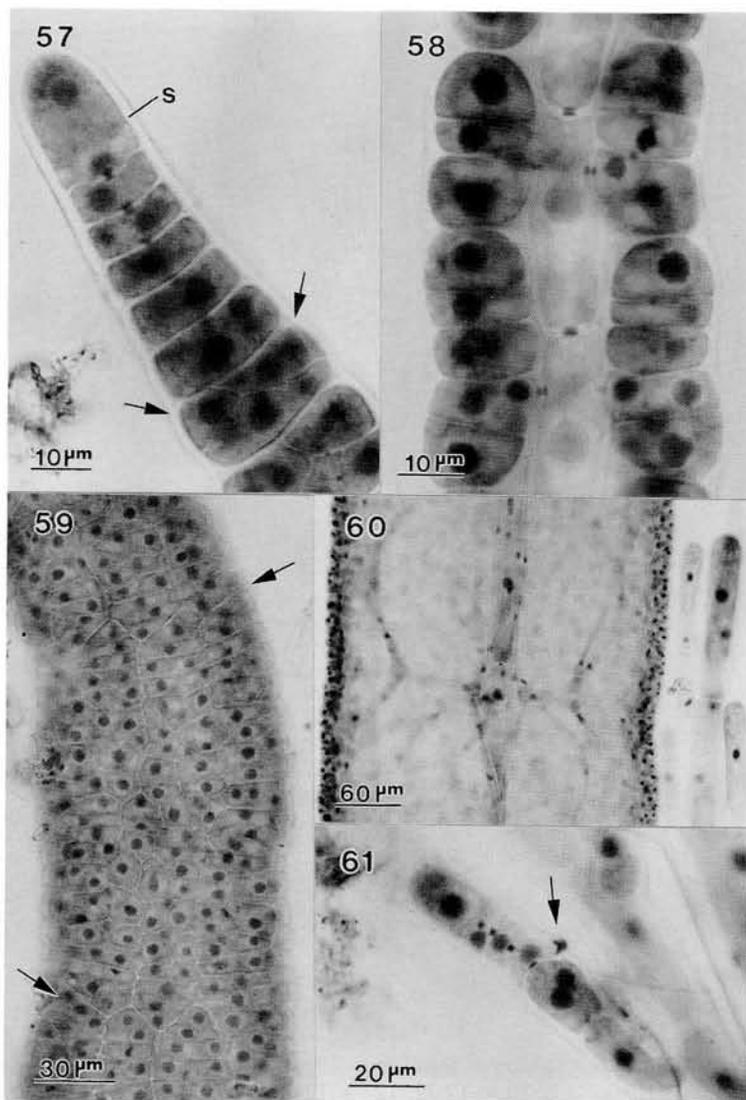
descending filaments and ray cells undergo anticlinal and periclinal divisions (Fig. 12-58) to produce a pseudoparenchymatous cortex. Growth of a segment of the cortex occurs in concert with the elongation of the axial cell that bears it. Regions of the cortex derived from adjacent axial segments abut, forming a confluent surface (Fig. 12-59). As a segment of the axis matures, periaxial cells and inner cortical cells elongate, pushing the cortex out and creating a hollow space between the axial filament and the surface of the thallus (Fig. 12-60). Species in which the gametophyte is branched cut off indeterminate lateral initials from an axial cell near the apex or from the surface of the developing cortex (Atkinson 1890).

The gametophyte of *Lemanea australis* is initiated directly from the pseudochantrancia stage following a presumed meiosis (Fig. 12-61). Nuclear divisions in cells of the pseudochantrancia stage resemble mitosis in Acrochaetiales (Figs. 12-62 to 12-65). Division takes place within the basal half of the dividing cell, orientation of the metaphase plate is variable but most often oblique, the chromosomes are often arranged in a ring at metaphase and anaphase, and there is a tendency toward precocious initiation of the septum as a septal ring. Nuclear divisions throughout the gametophyte resemble those in indeterminate filaments of *Batrachospermum boryanum* (Figs. 12-66 to 12-68). Division takes place at the site of subsequent septum formation, and the metaphase plate is oriented parallel



Figs. 12-57, 12-59. *Lemanea australis* (North Carolina). 12-57: Apex. 12-59: Cross section; axial cell bearing six periaxial cells.

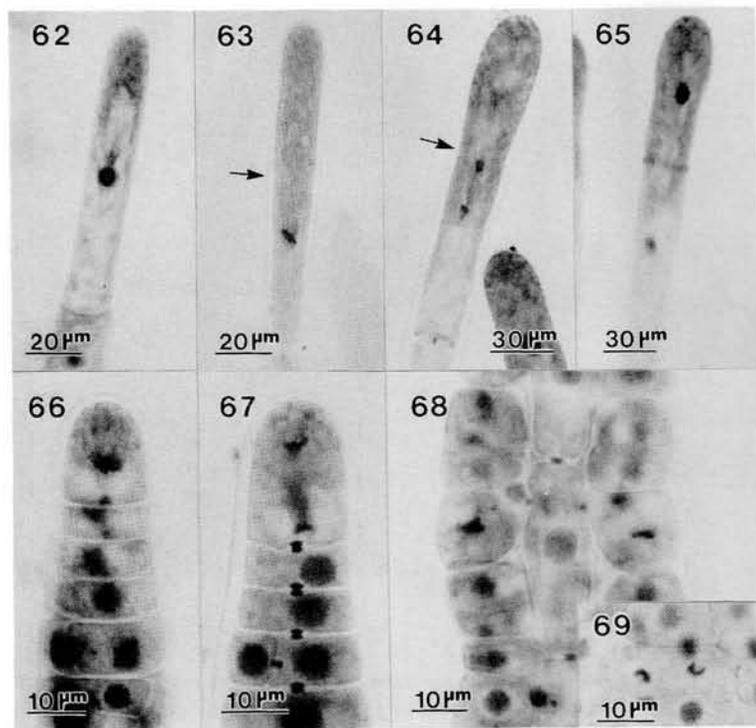
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Figs. 12-57 to 12-61. *Lemanea australis* (North Carolina). 12-57: Apex. Cytokinesis in the apical cell; septum (s) grows centripetally. Behind the apex a periaxial cell has cut off initials of ascending files (arrows). 12-58: Optical longitudinal section. Ascending and descending files have been initiated. 12-59: Surface of thallus; ascending and descending files abut (arrows). 12-60: Optical longitudinal section; periaxial cells and their lower order derivatives have elongated. 12-61: Gametophyte axis has been initiated on a short lateral branch of pseudochantransia stage following a presumed meiosis, leaving two polar bodies (arrow).

to the ensuing crosswall (Fig. 12-68). This pattern is slightly altered in apical cells of indeterminate filaments, where the orientation of division is slightly oblique but the subsequent septum is normally transverse (Figs. 12-66, 12-67). The tilt of the metaphase plate is such that during anaphase

migration the basal set of daughter chromosomes moves to the side of the incipient axial segment from which the first periaxial cell will be cut off. The chromosomes are at times arranged in a ring at metaphase and anaphase (Fig. 12-69), a feature that was noted by Mullahy (1952).



Figs. 12-62 to 12-69. *Lemanea australis* (North Carolina). 12-62: Pseudochantrasia, prophase. 12-63: Pseudochantrasia, tilted metaphase proximal to the precocious septum (arrow). 12-64: Pseudochantrasia, midanaphase. Division is just proximal to the precocious septum (arrow); apical set of daughter chromosomes in polar view forms a ring. 12-65: Pseudochantrasia, cytokinesis. Highly concavo-convex septum cuts into basal daughter cell. 12-66: Slightly tilted metaphase plate; apex of gametophyte. 12-67: Late anaphase; apex of gametophyte. 12-68: Metaphase in initials of descending files. 12-69: Late anaphase; thallus surface. Daughter chromosomes form partial rings.

The Thoreaceae contains the multiaxial genera *Thorea* and *Nemalionopsis*. In *Thorea ramosissima*, growth of indeterminate filaments is reported to be cellulose sympodial (Swale 1962).

IV. HIGHER FLORIDEOPHYCIDAE: GELIDIALES, BONNEMAISONIALES, GIGARTINALES, RHODYMENIALES, AND CERAMIALES

A. Mitosis and cytokinesis

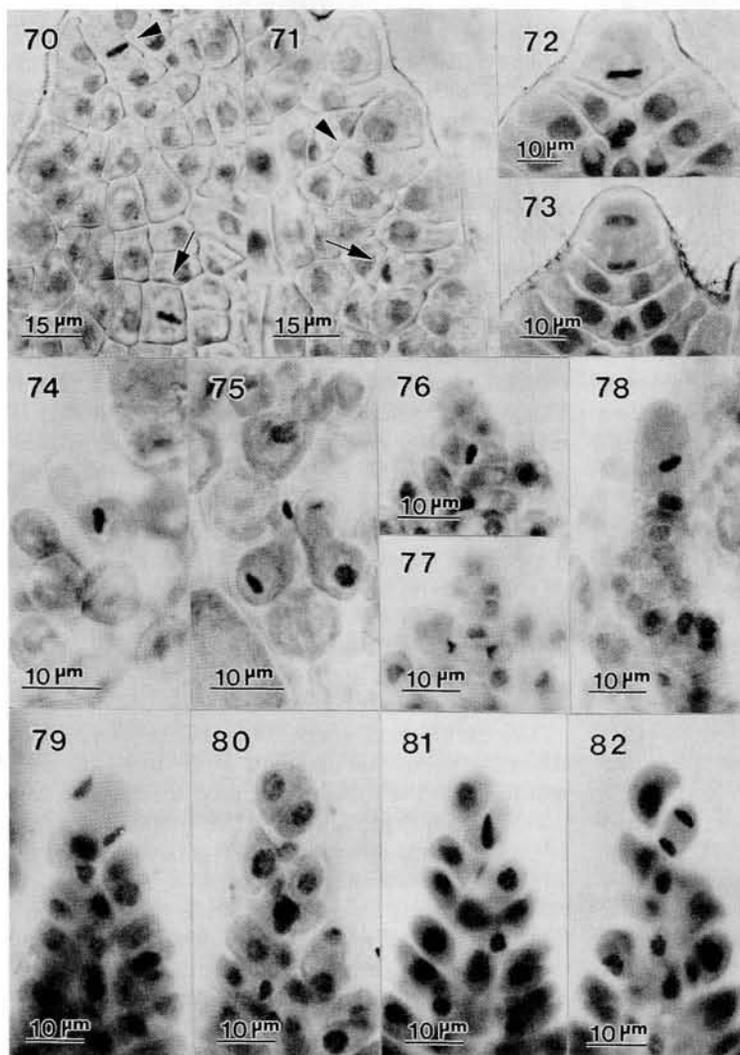
A common mode of mitosis and cytokinesis occurs in representatives of the Gelidiales, Bonnemaisoniales, Gigartinales, Rhodymeniales, and Ceramiales. Nuclear division takes place at the future site of septum formation, and the metaphase plate is

oriented parallel to the ensuing crosswall (Figs. 12-70 to 12-72, 12-74, 12-76, 12-78, 12-81). L'Hardy-Halos (1971) has commented on this behavior in the Ceramiaceae. This pattern of development occurs in both determinate and indeterminate filaments. At metaphase and anaphase the chromosomes are normally arranged in a linear band. During anaphase the two sets of daughter chromosomes migrate perpendicular to the plane of the preceding metaphase plate, moving to opposite ends of the dividing cell (Figs. 12-71, 12-73, 12-75, 12-77, 12-79, 12-82). A vacuole appears late in anaphase that separates daughter nuclei at telophase and maintains separation during cytokinesis. A septum is initiated after the completion of nuclear division that grows by annular furrowing.

The orientation of nuclear division is oblique



Figs. 12-figures in Subapical anaphase phase an Figs. 12-filament. formation plate, ap Figs. 12-apical ce indeterm initiating filament.



Figs. 12-70 to 12-73. *Membranoptera alata* (Nova Scotia). 12-70: Metaphase figures in apical (arrowhead) and subapical (arrow) cells of determinate filaments. Subapical cell forming an abaxial derivative. 12-71: Metaphase (arrowhead) and anaphase (arrow) in subapical cells of determinate filaments. 12-72, 12-73: Metaphase and anaphase in apical cell of indeterminate axial filament.

Figs. 12-74 to 12-78. *Crouania attenuata* (Florida). 12-74: Metaphase, determinate filament. 12-75: Anaphase, determinate filament. 12-76: Metaphase, periaxial cell formation. 12-77: Anaphase, periaxial cell formation. 12-78: Tilted metaphase plate, apical cell of indeterminate filament.

Figs. 12-79 to 12-82. *Rhabdonia coccinea* (Tasmania). 12-79: Late anaphase; apical cell of indeterminate filament. 12-80: Recently divided apical cell of indeterminate filament. 12-81: Metaphase; subapical cell of indeterminate filament initiating a single periaxial cell. 12-82: Anaphase; subapical cell of indeterminate filament.

in apical cells of indeterminate filaments of many genera (Fig. 12-78). When this occurs, the tilt of the metaphase plate is such that at anaphase the basal set of daughter chromosomes migrates to the side of the incipient subapical segment from which the first periaxial cell will be cut off (Figs. 12-79 to 12-82). The septum that forms following nuclear division is tilted correspondingly. The wedge-shaped segmental cell that results cuts off the first periaxial cell from its high or long side.

B. Development of prostrate systems

Guiry (Chapter 14) recognizes five types of spore germination, most of which occur in several orders of red algae. Spore germination is bipolar, leading to the early differentiation of an erect thallus and basal rhizoidal system in Ceramiales (Dixon 1973; Fritsch 1945) and a few species of Bonnemaisoniales (Chihara 1961). By contrast, most red algae produce an initial prostrate basal system from which one or more erect thalli may later develop. In many genera the prostrate system forms an extensive crust of varying thickness before initiating one or more upright axes; in others either the tetrasporophyte or both the gametophyte and tetrasporophyte are entirely crustose (West & Hommersand 1981).

Crustose prostrate systems arise in one of two ways: Either the attached spore divides perpendicular to the substrate one or more times and the resultant cells form lateral protuberances that are cut off as apical initials of prostrate filaments (*Naccaria*-type) or, following one or more divisions perpendicular to the substrate, horizontal divisions take place to produce a hemispherical mass of cells within the original cell wall (*Dumontia*-type). In the first instance the crust is initially monostromatic; in the second it is polystromatic from its inception (Chapter 14). The *Naccaria*-type germination pattern predominates in Bonnemaisoniales and in many of the more primitive members of the Gigartinales; the *Dumontia*-type is more common in advanced members of the Gigartinales and in Rhodymeniales.

The prostrate phase of *Bonnemaisonia asparagoides* is pinnately branched when growing attached to the substrate but is sparsely and irregularly branched, and bears numerous gland cells when growing free (Rueness & Åsen 1982). Uniaxial prostrate filaments bearing paired opposite laterals are reported in *Delisea* (Chihara 1961), *Humbrella hydra* (Hawkes 1983), *Calosiphonia vermicularis* (Mayhoub 1973, 1975), and *Schmitzia hiscockiana* (Maggs & Guiry 1985). *Dudresnaya japonica* (Umezaki 1968) has a

filamentous prostrate system that is predominantly unilaterally branched. In *Acrosymphyton purpuriferum* primary filaments of the prostrate system cut off pairs of lenticular cells from their apical pole that develop into lateral filaments. Later, additional lateral filaments may be formed from initials cut off at the antapical pole (Cortel-Breeman 1975). Very often an early filamentous stage develops into a fan-shaped polystromatic crust that has a monostromatic marginal meristem of creeping filaments. This is seen in *Acrosymphyton purpuriferum* (Cortel-Breeman 1975), *Gloiosiphonia verticillaris* (DeCew et al. 1981), *Farlowia mollis* (DeCew & West 1981), *Pikea californica* and *Schimmelmanna plumosa* (Chihara 1972). A pinnately branched, initially monostromatic crust has also been described for *Meredithia microphylla* (Guiry & Maggs 1985), *Cirrulicarpus carolinensis* (Hansen 1977), and several species of *Kallymenia* (Codomier 1972a, 1973a). The crusts of these three genera of Kallymeniaceae are unusual in that cells of neighboring filaments frequently fuse. Spores of *Sebdenia dichotoma* produce irregularly branched, monostromatic crusts and apical cells of filaments derived from different spores may fuse directly (Codomier 1973b).

Crusts of most species become polystromatic when the horizontal filaments of the basal system, referred to as the hypothallus, produce closely compacted ascending filaments, the perithallus. The hypothallus may bear rhizoids or even produce an inferior perithallus of descending filaments. A range of morphological types known from nature have been described by Denizot (1968).

Rietema and Klein (1981) have described the production of discoid microthalli that become polystromatic within a common sheath in *Dumontia contorta*. Radial growth of these disks takes place by a marginal meristem. Chen and Taylor (1976) followed the development of the *Dumontia*-type germling in *Chondrus crispus* with scanning electron microscopy. They observed that an extracellular sheath is produced prior to internal cell differentiation and suggest that this sheath is responsible for the discoid pattern of sporeling development.

C. Initiation of upright axes

The initiation of erect thalli from prostrate filaments or crusts has been reviewed by Gabrielson and Garbary (1986). In *Bonnemaisonia asparagoides*, which has a freely branched, filamentous prostrate system, erect axes originate as lateral initials that quickly become budlike and assume the form of the adult axis (Rueness & Åsen 1982). In *Gloiosiphonia*

erect axes are elongation and of individual periaxial cells (et al. 1981; M uprights develop (DeCew & W filamentous pro thin-walled ce (Hawkes 1983).

Kuckuck (1 multiaxial upright of perithallial initials that de of erect axes pattern of dev and other Fu *Platoma*-type been documented (1984). Here, produce uniaxial & Davis 1984 although cells of secondary are free and so

Secondary larly in both advanced fam as a mound c In uniaxial sp A tetrahedral been identified a primary axi (Kling & Boda erect thalli fr culture in m *chotoma* (Cod (Guiry & Mag G. *devoniensis* (Masuda et al the erect thal tissue that is trate system.

D. The erect

Several gener orders of Flor construction : *chospermum*, i ferentiation b whorled dete include *Atract Calosiphonia*, A

erect axes are initiated from the crust by rapid elongation and transverse divisions of apical cells of individual filaments. Subapical cells soon cut off periaxial cells that initiate cortical filaments (DeCew et al. 1981; Mohoroshi & Masuda 1980). Uniaxial uprights develop in a similar fashion in *Farlowia* (DeCew & West 1981). In *Hummbrella hydra* the filamentous prostrate system gives rise to enlarged, thin-walled cells before initiating uniaxial uprights (Hawkes 1983).

Kuckuck (1912) illustrated the initiation of the multiaxial upright thallus in *Platoma bairdii*. A group of perithallial cells simultaneously produce apical initials that develop in concert to generate a bundle of erect axes bearing cortical filaments. A similar pattern of development may occur in *Neurocaulon* and other Furcellariaceae (Codomier 1972b). The *Platoma*-type of multiaxial development has also been documented for *Dumontia contorta* (Rietema 1984). Here, the erect filaments can diverge to produce uniaxial side branches (Rietma 1984; Wilce & Davis 1984). *Schizymenia* is interesting in that, although cells of the crust interconnect by means of secondary pit connections, the erect filaments are free and separate (Ardré 1980).

Secondary pit connections are produced regularly in both prostrate and erect systems in more advanced families. The erect thallus often begins as a mound of tissue on the surface of the crust. In uniaxial species an apical initial is soon cut out. A tetrahedral initial with three cutting faces has been identified in *Gracilaria verrucosa* that produces a primary axis in a seemingly multiaxial thallus (Kling & Bodard 1986). The initiation of multiaxial erect thalli from crusts has been investigated in culture in many species, including *Sebdenia dichotoma* (Codomier 1973b), *Meredithia microphylla* (Guiry & Maggs 1985), *Gymnogongrus crenulatus* and *G. devoniensis* (Ardré 1978), and *Mastocarpus* sp. (Masuda et al. 1987). In these particular examples the erect thallus begins as a bulge or mound of tissue that is scarcely differentiated from the prostrate system.

D. The erect thallus: simple uniaxial types

Several genera belonging to the more advanced orders of Florideophycidae have a simple, uniaxial construction superficially similar to that of *Batrachospermum*, in which there is a high level of differentiation between indeterminate axes and the whorled determinate lateral filaments. Examples include *Atractophora* (Bonnemaisoniales), *Schmitzia*, *Calosiphonia*, *Acrosymphyton*, *Dudresnaya* and *Thure-*

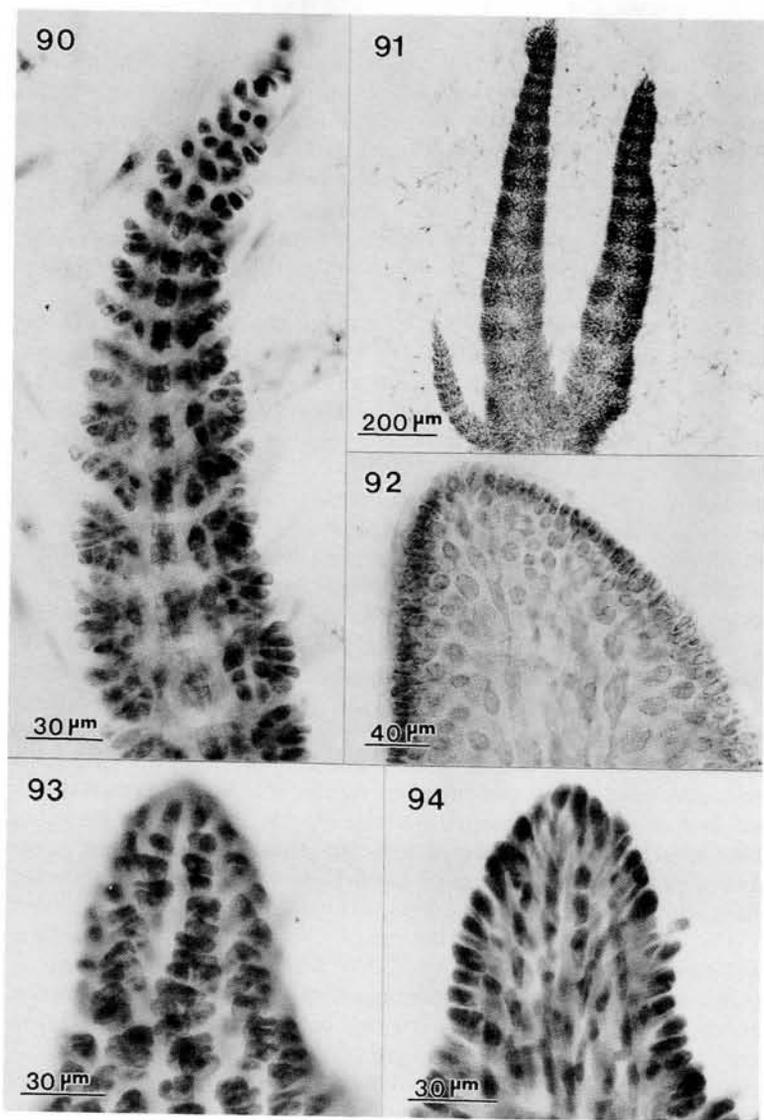
tella (Gigartinales), and *Crouania* and *Gulsonia* (Ceramiales) (Kylin 1956). In *Dudresnaya* cortical filaments are initiated two ways: some arise from the axis a few cells behind the apex, whereas others are produced secondarily from preexisting determinate filaments or from rhizoids (Kraft & Robins 1985).

Although *Crouania attenuata* is similar to *Batrachospermum* in its morphology (Fig. 12-83), mitosis and cytokinesis take place at the site of future septum formation in both indeterminate axes and determinate lateral filaments. In addition, the initiation of determinate lateral filaments and lateral indeterminate axes follows a regular pattern. Apical cells of indeterminate filaments divide transversely to cut off axial segments, each of which initiates three periaxial cells. The position of the first periaxial cells in successive segments describes a 40-degree spiral (Fig. 12-84). The second and third periaxial cells are cut off 120 degrees to the right and left of the first. During division the mitotic apparatus of an apical cell is tilted such that the basal set of daughter chromosomes will migrate to the side of the incipient subapical cell from which the first periaxial cell will be cut off (Figs. 12-85 to 12-88).

Nuclear divisions associated with periaxial cell formation take place at the juncture of the bud and the axial cell. The metaphase plate is oriented vertically, parallel to the lateral wall of the axial cell (Fig. 12-76). During anaphase one set of chromosomes moves out into the apical portion of the bud, the other back into the axial segment (Fig. 12-77), followed by formation of daughter nuclei and a septum.

During growth of determinate lateral filaments buds are formed as bulbous outgrowths from the distal end or shoulder of a cell. Division takes place just within the parent cell or at the juncture of the bud and the parent cell, and the metaphase plate is oriented perpendicular to the long axis of the initial (Fig. 12-74). During anaphase daughter chromosomes move perpendicular to the plane of the preceding metaphase plate (Fig. 12-75). When migration has ceased, daughter nuclei form and a septum develops by annular ingrowth.

Branching of the thallus is largely abaxial and follows a regular pattern. Most indeterminate axes bear an indeterminate lateral abaxially eight to fifteen segments from their base. A second indeterminate lateral is initiated two to six (most often four or five) segments beyond the first, also on the abaxial surface (Fig. 12-83). Indeterminate laterals tend to overgrow the parent axis (Fig. 12-83), as in *Crouania mucosa* (Wollaston 1968). This type of thal-
lus development has been termed ramisymphodial



Figs. 12-90, 12-91. *Gloiosiphonia capillaris* (Massachusetts, Newfoundland). 12-90: Optical longitudinal section. Determinate filaments form ascending, abaxially branched files (lateral derivatives out of focal plane). 12-91: Surface of thallus; each band is formed of the determinate filaments derived from a single axial cell. Figs. 12-92 to 12-94. *Agardhiella subulata* (North Carolina, New Jersey). 12-92: Longitudinal section. Determinate filaments form ascending, abaxially branched files. 12-93: Cortex formed of vertical sectors, each sector composed of the determinate lateral filaments of a single axial filament. 12-94: Optical longitudinal section of Fig. 12-93, showing indeterminate filaments.

first derivative of an axial cell is determined at the time the apical cell divides to cut off that axial cell. In many taxa of the Crouanieae, including some species of *Crouania*, indeterminate laterals either re-

place one of the whorled determinate laterals on a segment or are borne on the basal or suprabasal cell of a determinate lateral filament (Hommersand 1963; Wollaston 1968).

E. Organization of determinate lateral filaments

In many higher Florideophycidae branching of determinate lateral filaments is organized around a leading filament, and the filaments coalesce to form a well-defined cortex. Chadefaud (1952) referred to this tendency as "axialisation des pleuridies," "pleuridie" being the term given to the whorled determinate lateral filaments of algae like *Batrachospermum*. *Gloiosiphonia capillaris* exemplifies this type of thallus organization (Figs. 12-90, 12-91). Each axial cell initiates four periaxial cells; each periaxial cell undergoes repeated transverse divisions to produce a file of cells that ascends at a 30- to 50-degree angle. When three to four cells long, a determinate filament initiates laterals from its basal segments. Each segment of a primary determinate lateral filament gives rise to four derivatives: two laterally, one abaxially, and one basally. The basal derivative initiates a descending rhizoidal filament. The same pattern of branching is repeated by cells of higher order filaments, though initiation of a basal derivative ceases four to six cells from the axis. A mature determinate lateral filament normally contains eight to twelve orders of branches.

As a determinate filament matures, the inner two to four cells elongate, becoming columnar, the middle one to two enlarge to an intermediate size, and the outer four to six remain small and ovoid. The space created by the extension of the basal cells of the determinate lateral filaments becomes filled by a mass of thick-walled descending rhizoidal filaments (Fritsch 1945).

The basic pattern of development of determinate lateral filaments exhibited by *Gloiosiphonia capillaris* occurs in uniaxial and multiaxial genera throughout the advanced Florideophycidae. It is common in the Gelidiales, Gigartinales, and Rhodymeniales (see illustrations in Kylin 1956). In the Ceramiales it is found with modification in the Delesseriaceae. Here, the two lateral periaxial cells initiate determinate filaments that branch abaxially to form a monostromatic blade (Figs. 12-70, 12-71).

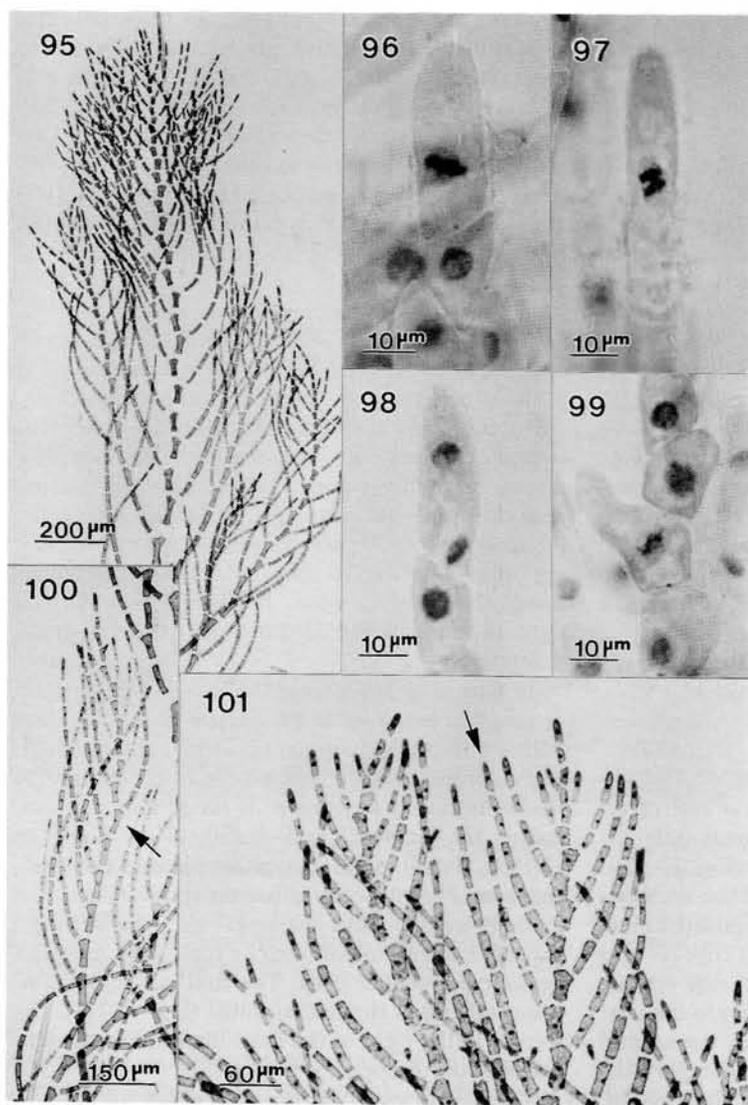
In multiaxial plants each segment of an indeterminate axial filament cuts off a limited number of periaxial cells (usually one or two) toward the thallus surface. Each initiates a determinate lateral filament that develops in the manner described (Fig. 12-92). In *Agardhiella subulata* only one periaxial cell is produced by each axial cell (Gabrielson & Hommersand 1982a) and the determinate lateral filaments derived from successive cells of a given indeterminate filament comprise a vertical sector of the cortex (Figs. 12-93, 12-94).

F. Facultative branching of the thallus

Many Rhodophyta initiate lateral indeterminate axes through a transformation of the apical cell of a determinate lateral filament. *Callithamnion byssoides* exhibits this behavior (Fig. 12-95). Divisions in apical cells of indeterminate filaments are oblique (Figs. 12-96 to 12-98). In material attributed to this species from North Carolina the tilt of the metaphase plate and ensuing crosswall shifts 180 degrees with each division, the high side of the resultant segments lying alternately to the left and right. There is no indication of spiral branching as in European *C. byssoides* (Dixon & Price 1981). Each segment of an indeterminate axis cuts off a single derivative from its high side following formation of a lateral bud (Fig. 12-99).

All laterals are initially determinate in their pattern of growth. Apical cells extend, then divide by means of a transverse septum. Some continue to grow in this manner, producing a file of transversely septate, unbranched segments (Fig. 12-95). In others the apical cell begins to divide obliquely in an alternate-distichous fashion after a variable number of segments have been formed. Lateral initials are cut off from the high side of each segment two to five cells behind the apex. Filaments that continue to grow in this manner produce an indeterminate lateral branch. A variety of irregular branching patterns are also encountered. In some cases a lateral filament will shift from an irregular pattern to the regular pattern characteristic of either indeterminate axes or determinate, unbranched filaments (Fig. 12-100). The lack of a clear distinction between determinate and indeterminate filaments in *Callithamnion* has been noted by Dixon (1973) and Hommersand (1963).

Konrad-Hawkins (1964a,b, 1968) has described a similar situation in *Callithamnion roseum*. During growth of some lateral filaments there is a shift from transversely septate, unbranched segments to obliquely septate segments that branch from their high side. Associated with this shift in the orientation of nuclear and cell division is a change in the length of the apical cell at the time of division, a change in the relative lengths of the daughter cells, and a decrease in the rate of elongation of the filament. This transformation appears to be involved in the regulation of thallus form (Konrad-Hawkins 1964b). A similar mechanism seems to operate in *C. byssoides*. Those lateral filaments whose rate of growth is greatest will tend to extend past their neighbors. It is these filaments that are transformed into indeterminate axes, slowing their growth rate



Figs. 12-95 to 12-101. *Callithamnion byssoides* (North Carolina). 12-95: Alternate-distichous branching of main axis, laterals showing variation in branching patterns. 12-96: Metaphase, apical cell of indeterminate filament. 12-97: Early anaphase, apical cell of indeterminate filament. 12-98: Telophase, apical cell of indeterminate filament. 12-99: Metaphase, formation of lateral initial. 12-100: Filament that has shifted (arrow) from unilateral to alternate-distichous branching. 12-101: Apical cells of lateral derivatives of two indeterminate filaments lie in a line; one (arrow) has shifted to oblique divisions.

and preserving a monopodial habit (Fig. 12-101).

Facultative branching has been described in two species of *Gelidium* (Dixon 1958) and appears to be the mechanism of branch initiation in many thalloid taxa, but individual cases are not well documented. In *Agardhiella subulata* indeterminate

branches are initiated at the thallus surface, and inner cortical cells directly below a branch primordium elongate, taking on the appearance of medullary cells (Gabrielson & Hommersand 1982a). Many taxa that produce indeterminate lateral branches in a regular pattern at the thallus apex also have

the ability to initiate indeterminate branches facultatively, a process often referred to as adventitious branching (Dixon 1960; Hommersand 1963).

G. Patterned branching of the thallus

In the complex thalli of some uniaxial genera there is a regular pattern to the initiation of lateral branches. Branches may develop similarly, as in *Microcladia* (Hommersand 1963), or there may be differentiation between axes of various orders (Cramer 1864; Dixon 1973). In the *Dasyaceae* the regular arrangement of laterals is a result of cellulosympodial development (L'Hardy-Halos 1968, 1971). Some advanced *Florideophycidae* initiate axes of limited growth, here referred to as determinate branches, in addition to determinate lateral filaments and indeterminate lateral branches. Determinate branches are produced in a prescribed arrangement on indeterminate axes and exhibit a regular pattern of development distinct from that of the indeterminate axes that bear them. This is commonly seen in the *Bonnemaisoniales* and *Ceramiales* and also occurs in certain uniaxial *Gigartinales* (Chihara & Yoshizaki 1972; Dixon 1973; Hommersand 1963; Kylin 1956; Scagel 1953).

In *Bonnemaisonia hamifera* the apical cell of an indeterminate filament cuts off segment cells basally by means of oblique crosswalls (Fig. 12-102). The plane of division and high side of the resultant segment cells describe a three-eighths spiral (Chihara 1961; Kylin 1928). Each axial segment cuts off two periaxial cells: the first from the high side shortly after formation of the segment and prior to the next division of the apical cell (Fig. 12-103), the second much later, opposite the first. The first periaxial cell initiates a determinate branch or short shoot. The apical cell of a determinate branch undergoes slightly oblique divisions (Fig. 12-104). The tilt is such that the abaxial side of the newly formed subapical segment is longer than its adaxial side. Each segment of a determinate lateral branch cuts off three periaxial cells, the first abaxial (Figs. 12-105, 12-106), the second and third adaxial. Each undergoes a series of divisions to form cortex.

The fate of the second periaxial cell of an indeterminate axial segment is variable (Chihara 1961). In female plants it may produce a fertile branch (Fig. 12-102) that bears a carpogonial branch on its fifth or sixth segment, arresting development. Alternatively, it can produce an indeterminate lateral branch that may remain dwarfed or may develop into a major branch of the thallus. When

neither a fertile branch nor an indeterminate lateral is produced, the second periaxial cell divides to form cortex.

Development of the thallus is similar in other *Bonnemaisoniaceae*. There is variation in the arrangement of first periaxial cells on successive axial segments, and thus in the arrangement of determinate branches, and in the mode of initiation of indeterminate lateral branches (Chihara & Yoshizaki 1972).

A similar situation is encountered in *Phacelocarpus* (*Gigartinales*) (Searles 1968). Each axial cell cuts off four periaxial cells. The first periaxial cell initiates a determinate branch, the second, third, and fourth give rise to determinate filaments that corticate the axis. In most species there is a 180-degree rotation between first periaxial cells in successive segments, and the determinate branches, often termed teeth, are distichous. In others they are spirally arranged. When the thallus branches either the second, third, or fourth periaxial cell initiates an indeterminate lateral filament that forms a new axis.

In most *Rhodomelaceae* the thallus is composed of axes that bear two or more types of laterals, each with a distinct developmental pattern (Fig. 12-107). In *Polysiphonia harveyi* apical cells of indeterminate filaments divide by means of an oblique septum, cutting off segmental cells basally (Figs. 12-108 to 12-110). The tilt of the metaphase plate and ensuing crosswall describes a one-quarter spiral. When two to three cells behind the apex, an axial segment cuts off a lateral initial from its high side, followed by four pericentral cells. The first pericentral cell is cut off below the lateral initial (Fig. 12-111), the second to the right of the first, the third to the left, and the fourth opposite the first.

The lateral initial gives rise to either an indeterminate lateral branch or a trichoblast. Development of indeterminate lateral branches is identical to the parent axis after the initial three to five segments. Trichoblasts are uniseriate and deciduous. They develop monopodially but appear dichotomously branched at maturity (Fritsch 1945, p. 545). In some species of *Polysiphonia* indeterminate laterals are borne on the basal cell of a trichoblast. Most *Rhodomelaceae* possess trichoblasts, though they are absent in some genera (Hommersand 1963). In some *Rhodomelaceae* determinate branches analogous to the short shoots of *Bonnemaisoniales* are produced in addition to trichoblasts, indeterminate laterals, and pericentral cells (Falkenberg 1901; Kylin 1956).

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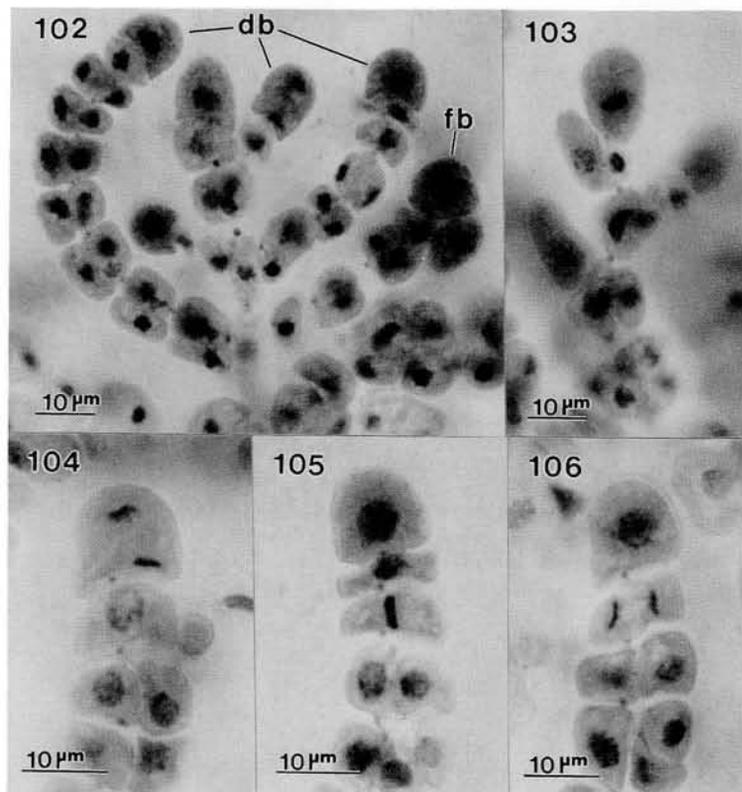
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Figs. 12-102 to 12-106. *Bonnemaisonia hamifera* (Maine). 12-102: Apex of indeterminate axis bearing determinate branches (*db*) and a fertile female branch (*fb*). 12-103: Metaphase, apical cell of indeterminate filament. 12-104: Anaphase, apical cell of determinate branch. 12-105: Metaphase, axial cell of determinate branch. Initiation of abaxial derivative. 12-106: Anaphase, axial cell of determinate branch. Initiation of abaxial derivative.

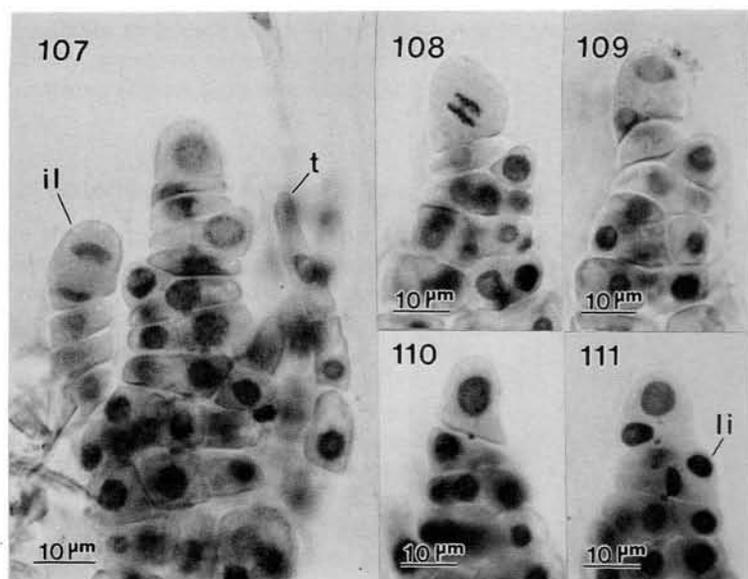
site of initiation of determinate filaments, determinate branches, and sometimes indeterminate branches is controlled by a precise pattern of cell divisions at the apex of an indeterminate filament. Development of each type of filament and branch is in turn controlled at its apex by the pattern of division. Maturation is largely a result of precise patterns of cell division and cell enlargement behind the apex.

H. Secondary pit connections, wall growth, and increasing nuclear volume

Secondary pit connections are formed as a result of the fusion of conjunctor cells with adjacent vegetative cells in most higher Florideophycidae. Vegetative fusions and secondary pit connections are absent in genera having the simplest thallus con-

struction, found in the Naccariaceae, Dumontiaceae (Robins & Kraft 1985), Nemastomataceae (Kraft 1975; Kraft & John 1976), Calosiphoniaceae (Feldmann 1954), and Ceramiaceae (Fritsch 1945).

In uniaxial genera and the lateral margins of multiaxial genera secondary pit connections are most often formed basipetally and laterally between intercalary cells of adjacent determinate lateral filaments (Figs. 12-112, 12-113). In multiaxial genera adjacent indeterminate axial filaments become linked, either directly by means of secondary pit connections or through interconnecting filaments (Chiang 1970; Gabrielson & Hommersand 1982a,b; Kraft 1977; Lee 1978). The axial cells of *Agardhiella* contain large numbers of nuclei (Fig. 12-114), most likely as a result of fusion with multinucleate cells analogous to conjunctor cells. Although it has been thought that secondary pit connections are absent



Figs. 12-107 to 12-111. *Polysiphonia harveyi* (North Carolina). 12-107: Apex bearing indeterminate lateral branch (*il*); apical cell in telophase and trichoblast (*t*). 12-108: Anaphase, apical cell of indeterminate filament. 12-109: Telophase, apical cell of indeterminate filament. 12-110: Oblique septum, apex of indeterminate filament. 12-111: Axial segment has cut off a lateral initial (*li*), in metaphase of division that will produce the first periaxial cell.

in *Bonnemaisoniales* (Fritsch 1945), in *Bonnemaisonia hamifera* they are formed between the cortical cells of both indeterminate axes and determinate branches (Fig. 12-115; Coomans 1986). The benefits of vegetative fusions resulting in secondary pit connections include increased structural integrity and new avenues of vegetative modification.

In many higher Florideophycidae cells of both axial and determinate lateral filaments increase greatly in size during maturation. Cell enlargement continues well behind the apex, and cells can reach many times their original volume (Dixon 1971, 1973). Wall growth associated with the elongation of intercalary cells has been investigated in several genera of Ceramiaceae (Chapter 11) and was found to be localized in unipolar or bipolar bands.

As Magne (1964) has noted, Florideophycidae tend to maintain a fairly constant ratio of nuclear volume to cell volume. Increasing the number of nuclei in a cell as it enlarges through the formation of secondary pit connections is one strategy employed to accomplish this objective. In other taxa nuclear divisions take place within intercalary cells without ensuing cell divisions, leading to the production of multinucleate cells (Goff & Coleman 1986;

L'Hardy-Halos 1971). An increase in cell volume is also achieved by increasing the size of a single nucleus. This is seen in axial cells of *Bonnemaisonia hamifera* (Fig. 12-116) and in numerous other taxa that lack secondary pit connections or in which the formation of secondary pit connections is restricted to the cortex. Single nuclei that enlarge in conjunction with cell enlargement are common in Ceramiaceae (L'Hardy-Halos 1971). Axial cells of *Portieria hornemannii* (formerly *Chondrococcus hornemannii*; see Silva et al. 1987) combine these two behaviors: sub-apical cells become multinucleate through nuclear divisions in the absence of cell division, and the nuclei produced enlarge in conjunction with growth of the axial cell (Fig. 12-117).

That there is an actual increase in the amount of DNA associated with the observed increase in nuclear volume has been demonstrated through quantitative microspectrofluorometry (Goff & Coleman 1984, 1986; Chapter 3). Increase in nuclear DNA content in association with an increase in nuclear volume may prove to be the norm in those algae in which there is extensive cell enlargement in the absence of internal nuclear divisions or the formation of secondary pit connections.

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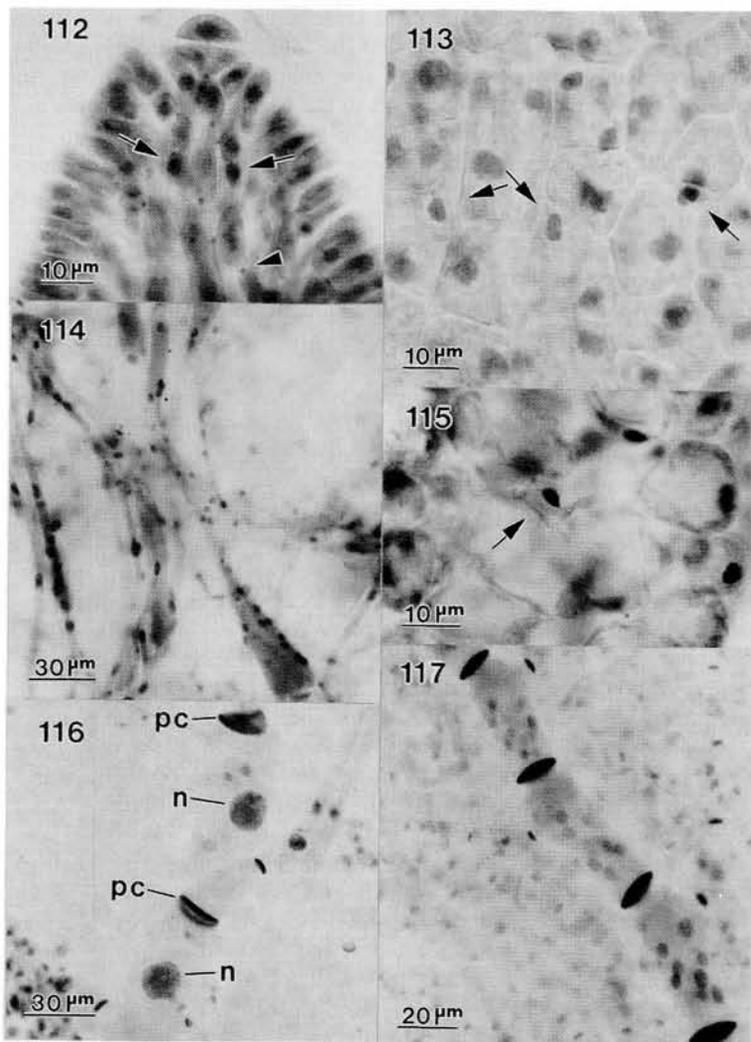


Fig. 12-112. *Gelidium crinale* (North Carolina). Junctor cell (arrows) cut off from periaxial cell will fuse with subtending periaxial cell, forming a secondary pit connection (arrowhead).

Fig. 12-113. *Membranoptera alata* (Nova Scotia). Junctor cell (arrows) fusing with subtending cell, depositing nucleus and forming secondary pit connection.

Fig. 12-114. *Agardhiella subulata* (North Carolina). Multinucleate axial cells.

Figs. 12-115, 12-116. *Bonnemaisonia hamifera* (Maine). 12-115: Junctor cell fusing with adjacent cortical cell (arrow). 12-116: Axial cells with enlarged nuclei (n) and pit connections (pc).

Fig. 12-117. *Portieria hornemannii* (South Africa). Axial cells, each with many enlarged nuclei.

V. SUMMARY

We recognize three major groups in the Rhodophyta based on features of vegetative morphology and development: the Bangiophycidae; the lower Florideophycidae, consisting of the Acrochaetiales,

Nemaliales, and Batrachospermales; and the higher Florideophycidae, containing the Gelidiales, Bonnemaisoniales, Gigartinales, Rhodymeniales, and Ceramiales.

The Bangiophycidae form a closely knit group based on features of mitosis and vegetative de-

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velopment. Filamentous growth characterizes the earliest stages of thallus development in most Bangiophycidae. Growth takes place through strictly apical or both apical and intercalary cell divisions. In many taxa diffuse growth, with the formation of true parenchyma, characterizes the mature thallus. The thallus is filamentous and growth is apical in *Rhodochaete* (Rhodochaetales) and probably in the conchocelis phase of *Bangia* and *Porphyra* (Bangiales). These also possess simple pit plugs, and the latter have cellulose as the principal fibrillar wall component. It may be that the filament is the ancestral unit of thallus construction in extant Bangiophycidae, and a unicellular or colonial habit, parenchyma, and even intercalary growth represent derived conditions associated with changes in cell wall composition and the absence of pit connections.

Patterns of mitosis and cytokinesis are similar in all orders of Bangiophycidae. Distinguishing features include an extended nucleus at prophase, the aggregation of the chromosomes into a ring during metaphase and anaphase, a greatly extended interzonal spindle during late anaphase, the involvement of the chloroplast and pyrenoid in maintaining separation of daughter nuclei during telophase and cytokinesis, and septation by means of a broad cleavage furrow.

The Florideophycidae are filamentous in construction, and growth is apical with few exceptions. Evolutionary advances in vegetative organization have taken place within the bounds of these developmental constraints. The lower Florideophycidae is a distinct assemblage characterized by the presence of one or more acrochaetoid stages in the life history, filaments that exhibit a primitive type of mitosis, cytokinesis and growth, and similarities in pit plug ultrastructure (Chapter 2) and post-fertilization development (Chapter 13). The relationships between the orders grouped as the higher Florideophycidae are less certain. They may represent several evolutionary lines with parallel modifications of thallus construction (Chapter 18).

In the Acrochaetales, Nemaliales, determinate lateral filaments of *Batrachospermum* and pseudochantransia stage of *Lemanea* (Batrachospermales) growth takes place through a process best described as budding. Meristematic cells initiate apical or lateral buds. Buds may be conspicuous, as in the determinate filaments of *Batrachospermum* and *Liagora*, or indistinguishable, as in *Audouinella*. Nuclear division takes place in the body of the parent cell. There is no relationship between the location of nuclear division and the site of cytokinesis. Mitosis here resembles that in the Bangiophycidae. The

chromosomes are arranged in a ring at metaphase and anaphase, and the interzonal spindle is greatly extended during late anaphase and telophase. In contrast to mitosis in the Bangiophycidae, there are two distinct stages to anaphase, the second involving migration of one set of daughter chromosomes into the apical or lateral bud. In addition, division occurs around an enlarging basal vacuole rather than a central chloroplast and pyrenoid. New wall deposition is strictly apical in *Audouinella* (Acrochaetales) and cell elongation is completed a few cells behind the apex. The same appears to be true of *Rhodochaete*.

The freely branched, loosely organized determinate filaments of *Batrachospermum* are replaced in *Lemanea* by a confluent cortex composed of filaments that follow a prescribed pattern of development. Associated with this change is a shift from the budding process of *Batrachospermum* to growth by means of cell expansion and cleavage in *Lemanea*, and mitosis becomes located at and oriented perpendicular to the plane of the ensuing crosswall.

The advent of morphologically and developmentally distinct axes was a major step in the evolution of thallus form. A central axis characterizes thallus construction in *Batrachospermum* and *Lemanea* among lower Florideophycidae and predominates in the higher Florideophycidae. Axial filaments are indeterminate and normally bear determinate lateral assimilatory filaments. Distinct patterns of mitosis and cell maturation are associated with the growth of axial filaments. Nuclear division is located at and oriented perpendicular to the ensuing crosswall plane. Cell enlargement continues well behind the apex, axial cells increasing greatly in length and diameter during maturation. Where known, growth of axial cells occurs through localized deposition of new wall material. Unipolar or bipolar band growth has been documented in *Batrachospermum* and several genera of Ceramiaceae.

In the higher Florideophycidae nuclear division takes place at the future site of cytokinesis, and the metaphase plate is oriented parallel to the plane of the ensuing septum. The chromosomes are arranged in a linear band during metaphase and anaphase, and anaphase migration is perpendicular to the plane of the preceding metaphase plate. This is true of divisions in determinate lateral filaments as well as indeterminate axial filaments. Axial filaments exhibit patterned development, established at the apex by the plane of division of the apical cell. In many taxa, especially those with radial symmetry, the metaphase plate is tilted such that the basal set of

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daughter chromosomes migrates to the side of the incipient axial segment from which the first periaxial cell will be cut off. Often, the first periaxial cell on successive segments describes a spiral, and subsequent periaxial cells on a given axial segment are cut off in a regular sequence.

In many Ceramiales, Bonnemaisoniales, and uniaxial Gigartinales the position of lateral branches, as well as determinate filaments, is determined by the pattern of division at the apex. Lateral branch initials are cut off prior to ordinary periaxial cells in many Ceramiaceae, as are trichoblast and branch initials in many Rhodomelaceae. A similar, but more complex behavior is seen in the Bonnemaisoniaceae and several families of the Gigartinales. In all of these cases the location of lateral initials is determined by the orientation of the mitotic apparatus at the time the axial segment that bears them is cut off. In other higher Florideophycidae branching of the thallus is facultative, involving a transformation of the apical cell of a determinate filament into the initial of an indeterminate axis.

The most primitive genera of the higher Florideophycidae have whorled determinate lateral filaments that develop equally, as in *Batrachospermum*. Evolution of the cortex has led to the establishment of a primary, ascending filament. Cells behind the apex of a primary filament initiate lateral, abaxial, and basal derivatives. This pattern of cortical development is common in the Gigartinales. There is also a shift from budding and filamentous growth to cell expansion and cleavage. Further modification involves the reduction or loss of certain of these filaments and changes in patterns of cell maturation.

A variety of mechanisms that effect an increase in nuclear volume, and presumably ploidy level, are associated with the extensive cell enlargement that takes place in the axial and determinate lateral filaments of higher Florideophycidae. This is accomplished through an increase in the size of nuclei, the number of nuclei, or both. Increased numbers of nuclei result from nuclear divisions without accompanying cell divisions or from the formation of secondary pit connections. The ability to form secondary pit connections by means of vegetative cell fusions, a behavior restricted to the higher Florideophycidae, expands the potential for thallus modification.

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