

Sexual reproduction and cystocarp development

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I. THE SEXUAL SYSTEM

Sexual reproduction is oogamous in red algae and involves the union of a nonflagellated male gamete, the spermatium, with a receptive process, the trichogyne or protrichogyne, at the distal end of a special female cell, the carpogonium. Life histories of sexually reproducing members of the Bangiophycidae are variously interpreted as biphasic or triphasic at the present time (e.g., Cole & Conway 1980; Gabrielson & Garbary 1986; Guiry 1987). The cytological studies of Yamanouchi (1906) on *Poly-siphonia* and of Magne (1964, 1972) on genera having a heteromorphic life history established a fundamental linkage between the sexual system of the Florideophycidae and a life cycle consisting of three phases: a haploid sexual phase, the gametophyte, a diploid phase that develops directly on the female thallus, the carposporophyte, and a free-living diploid phase bearing meiosporangia, the tetrasporophyte. Most modified life histories encountered in field and laboratory studies during the past 20 years are thought to be derived secondarily from the triphasic life cycle (See Dixon 1973; Guiry 1987; Magne 1972; West & Hommersand 1981).

Starting with the premise that a successful life history tends to maximize the potential for genetic recombination and genetic diversity from the union of a single pair of gametes, Searles (1980) concluded that selection has favored the evolution of a triphasic life history in red algae as compensation for an inefficient fertilization in the absence of motile gametes. The retention of the carposporophyte and its nourishment by the gametophyte are essential components of this adaptation, which balances the ability of the gametophyte to supply nutrients to the carposporophyte and the ability of the carposporophyte to utilize these nutrients effectively for reproduction.

The morphological manifestation of this nutrient-driven interaction between gametophyte and carposporophyte generations is the structure known as the cystocarp. The term "cystocarp" was first proposed by Kützing (1843, p. 100) as a substitute for "capsule", a name given to the larger of the two fruiting bodies found in red algae, and was adopted by J. Agardh (1844, p. 12), with some debate as to its interpretation. In the final analysis J. Agardh (1880, p. 168) came to regard the cystocarp as a complex structure consisting of an interior part (nucleus) and an exterior part (pericarp). He distinguished between external pericarp modified

from pigmented cortical tissue and internal pericarp modified from colorless subcortical or medullary tissue. Where a cellular pericarp was absent, as in *Ceramium* or *Halymenia*, the cystocarp was said to consist of the naked nucleus alone.

Schmitz (1883, pp. 243–6) was the first to distinguish clearly between the carpospore-bearing filaments that develop either directly from the carpogonium following fertilization or from an "auxiliary cell" after being contacted by an "ooblast cell" (connecting cell) or "ooblast filament" (connecting filament) and the vegetative tissue of the female plant. Later, Schmitz (1892, p. 17) and Schmitz and Hauptfleisch (1896, p. 303) called these filaments gonimoblasts.

In 1954 Drew adopted the term "carposporophyte" for the phase of development initiated by fertilization that leads to the production of filaments bearing sporangia. The carposporophyte is thus equivalent to all connecting cells, connecting filaments, and gonimoblasts whose development, barring apomixis, is correlated with the event of fertilization. In keeping with Drew's concept, the cystocarp consists of a diploid generation, the carposporophyte, produced from a fertilized carpogonium, together with any gametophytic tissues that may become specially modified for a supporting or protective role.

Classical studies of sexual reproduction in red algae are documented in the standard references of Fritsch (1945), Kylin (1956), and Oltmanns (1922). Recently, Silva and Johansen (1986) reviewed and analyzed the conceptual basis for the sexual systems evolved by Schmitz and Kylin for classifying the red algae. Information published since Kylin can be found in Dixon (1973), Drew (1954), Kraft (1981), Papenfuss (1966), and numerous papers on special taxa.

In the present chapter we will trace the stages of cystocarp development from the time of gamete production and fertilization to the formation and release of the carpospores. We will consider the role of the fertilized carpogonium and of auxiliary cells in gonimoblast formation and document the major evolutionary tendencies in cystocarp morphology and development, with examples taken from representative families. Finally, we will propose a model to account for the functional relationship between carposporophyte and gametophyte generations, based on mechanisms that regulate the production and processing of nutrients by the gametophyte and their transfer to and utilization by the carposporophyte.

II. DEVELOPMENTAL HOMOLOGIES OF REPRODUCTIVE CELLS

The morphogenesis of male gametes (spermatia), female gametes (carpogonia), and sexually or asexually produced spores (monospores, carpospores, tetraspores, etc.) each observe patterns of differentiation that are highly conserved throughout the Rhodophyta. Moreover, spores of all types exhibit similar ultrastructural features at comparable stages of differentiation and may also share characters in common with gamete morphogenesis (Chapters 2 and 14).

The position of reproductive cells on the thallus during early stages of their transformation is another highly conserved character. Three different developmental patterns may be distinguished in red algae. Each type is diagnostic for a distinct evolutionary line. Two of these lines are presently placed in the Bangiophycidae, and the third composes the Florideophycidae. In the orders Rhodochaetales and Compsopogonales (including Erythropeltidales) reproductive cells are intercalary. Spermatia, carpospores, and monospores are cut out one at a time by a curved wall. The mother cell remains, and the process may be repeated (Kornmann 1984, 1987; Magne 1960). In the Bangiales spermatia and carpospores are formed in packets by a series of successive divisions of the mother cell that are perpendicular to one another. The process is the same whether the spores are produced sexually or asexually (Cole & Conway 1980). Additionally, conchospores are generated in fertile cell rows and monospores are formed terminally in the filamentous conchocelis stage. In Florideophycidae, in sharp contrast to the Bangiophycidae, spermatangia, carpogonia, monosporangia, carposporangia, and tetrasporangia are all produced through transformation of apical initials. Only rarely are reproductive bodies intercalary in primitive genera belonging to this subclass (Gabrielson & Garbary 1986). Timing elements that determine the position of cells to be metamorphosed into spores or gametes are evidently conserved separately and expressed independently of elements that determine the type and function of the reproductive body produced.

III. LIFE HISTORIES AND THE ORIGIN OF THE CARPOSPOROPHYTE

The life history of *Bangia* and *Porphyra* (Bangiales) is biphasic according to Cole & Conway (1980). *Rho-*

dochaete (Rhodochaetales) is said to have a triphasic life history in which the zygote divides into two cells, one of which is released as a single carpospore (Guiry 1987). In our opinion, the life histories of all Bangiophycidae are biphasic and their fruiting bodies are neither equivalent to, nor prototypes of, the floridean carposporophyte.

Traditionally, the carposporophyte of Florideophycidae has been regarded as a somatic phase that develops directly on the female thallus from a zygote retained within the carpogonium (Dixon 1973; Drew 1955). Feldmann (1952) proposed that the original life cycle contained three morphologically identical, free-living generations: gametophyte, carposporophyte, and tetrasporophyte. This was succeeded by one in which the zygote, instead of being released immediately, divides within the carpogonium, giving rise to a carposporophyte that lives parasitically upon the gametophyte. The observation in a cultured strain of *Acrochaetium pectinatum* that the zygote either is released from the carpogonium as a "sporozygote" that can give rise to a free-living tetrasporophyte or develops in situ to produce an attached carposporophyte has been taken as evidence for Feldmann's original hypothesis (Abdel-Rahman & Magne 1983). Carrying the argument a step further, Magne (1972) suggested that evolution is regressive in red algae in such a way that any generation can potentially grow parasitically on the preceding one. Recently, Magne (1987) supported his proposal with a new evaluation of the life cycle of *Palmaria*, in which he interprets the erect diploid thallus as a free-living carposporophyte and the stalk cell and tetrasporangium as a reduced, parasitic tetrasporophyte.

Guiry (1987) rejected the hypothesis of a free-living carposporophyte generation and proposed that zygote amplification came about in two ways: (1) by formation of a mitosporangial generation and a meiosporangial generation (triphasic), or (2) by formation of a meiosporangial generation directly from the zygote (biphasic). In Guiry's model the in situ production of a carposporophyte (most Florideophycidae) or a tetrasporophyte (Palmariaceae and some Acrochaetiaceae) are alternative means of zygote amplification that are derived separately from the ancestral condition.

It is difficult in practice to distinguish between an ancestral biphasic life history and one that has arisen through secondary replacement of a carposporophyte with a tetrasporophyte. For example, in *Rhodochorton purpureum* the tetrasporophyte is said to develop from a clavate gonimoblast cell

(Stegenga 1978; West 1969), whereas in *Rhodothamniella floridula* the tetrasporophyte appears to develop directly from the fertilized carpogonium with only a single erect filament and one rhizoid (Stegenga 1978). The former could represent a reversal from a triphasic to a biphasic condition and the latter an ancestral biphasic life history.

In many Acrochaetiaceae clusters of branches bearing monosporangia, spermatangia, carposporangia, or tetrasporangia are similar in appearance. We suggest that the same or related genetic programs control branch formation and branching pattern in the development of all of these reproductive structures. Presumably, regulatory genes for the production of asexual filaments are expressed in the diploid zygote after the first one or two divisions. If so, the ancestral carposporophyte in Florideophycidae may be a somatic phase, as envisioned by Drew (1954), that is related fundamentally to an asexual fruiting structure bearing monosporangia, and it may be incorrect from a developmental standpoint to speak of *in situ* germination of a "retained zygote," "sporozygote," or "carpospore."

The ancestral carposporophyte must have been essentially autotrophic in its nutrition. This condition comes closest to being realized at the present time in the order Acrochaetiales. The evolution of the carposporophyte has been one of increasing dependency on the gametophyte. In primitive Florideophycidae it is the earliest stages of carposporophyte development that exhibit the greatest dependency. Nutritional dependency extended progressively to later stages in more advanced taxonomic groups. In the comparatively primitive genus *Nemalion* meristematic gonimoblast cells and carpospores both contain mature chloroplasts with pyrenoids that are substantially identical to plastids found in vegetative cortical filaments (Ramm-Anderson & Wetherbee 1982). In *Scinaia*, a more advanced member of the Nemaliales, developing carposporophytes contain proplastids that do not differentiate into functional chloroplasts until the carposporangia are cut off, and in *Bonnemaisonia* (Bonnemaisoniales) not even the differentiated chloroplasts of the mature carposporangia contain the number of thylakoids seen in vegetative or pericarpic cells (Ramm-Anderson 1983). The conversion of proplastids into mature, functional chloroplasts during carposporogenesis is a normal event in many advanced genera of red algae (Delivopoulos & Kugrens 1984; Delivopoulos & Tsekos 1986; Tsekos & Schnepf 1982; Wetherbee 1980).

IV. AUXILIARY CELL SYSTEMS

Whereas gonimoblasts are produced directly from the carpogonium in primitive Florideophycidae, carposporophyte development is mediated by one or more auxiliary cells in the advanced orders Gigartinales (including Cryptonemiales), Rhodomeniales, and Ceramiales. The carpogonium either produces connecting filaments or connecting cells or fuses directly with one or more auxiliary cells; either gonimoblasts are produced directly from the connecting filament in proximity to an auxiliary cell, or a diploid nucleus is transferred to the auxiliary cell, which in turn gives rise to the gonimoblasts.

Papenfuss (1951) and Drew (1954) distinguished between "nutritive auxiliary cells," which were said to have only a nutritive function, and "generative auxiliary cells," which were said to have both a nutritive and a generative function in that they produce the gonimoblasts. Our observations indicate that the nutrition of the carposporophyte and the regulation of its morphogenesis are separate functions carried out by different cell types that are distinguishable cytologically from one another. Accordingly, we will restrict the term "auxiliary cell" to cells that play a morphogenetic role in gonimoblast formation. All specialized structures that are strictly nutritive will be referred to as nutritive cells, nutritive filaments, or nutritive tissues.

In our opinion, auxiliary cells have evolved to perform two functions in support of zygote amplification: (1) as a site for the introduction of morphogenetic factors that either initiate gonimoblasts or transform their mode of development and (2) as an isolating mechanism operating at a second level that rejects incompatible or disharmonious fertilizations while allowing the rest to proceed.

In some respects an auxiliary cell resembles a carpogonium. Indeed, Schmitz (1883, p. 246) originally proposed that double fertilization occurs in Florideophycidae that possess auxiliary cells, a notion disproved by Oltmanns (1898), who showed that the nucleus derived from the fertilized carpogonium does not unite with the auxiliary cell nucleus. We have observed that, like the carpogonium, the auxiliary cell is granular in appearance with only small vacuoles present and that the nucleus possesses a conspicuous central nucleolus surrounded by a clear region, the hyaloplasm, and a faint network of chromatin (see Figs. 13-24, 13-94, 13-146). Walls of both are secondarily thickened with gelatinous material. The adherence of a con-

necting filament or connecting cell with an auxiliary cell, like the adhesion of spermatia to a trichogyne, appears to involve cell-specific interactions. Moreover, gonimoblasts produced in the vicinity of an auxiliary cell are often compact and branched like those formed directly from the carpogonium (see Section X).

In the past a distinction has been made between cases in which gonimoblasts develop from connecting filaments and those in which the diploid nucleus enters the auxiliary cell before gonimoblast initials are cut off. Recent studies have tended to downgrade the importance of this difference. For example, gonimoblasts develop directly from the auxiliary cell in *Predaea weldii*, whereas in most species of this genus they are produced from the connecting filament alongside the auxiliary cell (Kraft 1984).

Connecting cells are minute, uninucleate cells cut off by the carpogonium along with a minimal amount of cytoplasm. Typical connecting cells occur in only two orders: Ceramiales and Rhodymeniales. The nuclei are highly condensed and usually surrounded by a hyaline region just inside the cell membrane. A connecting cell expands only when contacted by an auxiliary cell. The behavior of a typical connecting cell is described and illustrated for *Polysiphonia* in Section IX.C.

Schmitz (1883, p. 245) regarded the "ooblast filament" (connecting filament) and the "ooblast cell" (connecting cell) as de novo structures. Drew (1954) interpreted the connecting filament as "primary gonimoblast" that gives rise to "secondary gonimoblast" once fusion with an auxiliary cell has taken place. In our opinion, connecting filaments, connecting cells, and auxiliary cells are structures that originated more than once and are polyphyletic.

The second role we attribute to auxiliary cells is that they function in rejecting disharmonious fertilizations. The experimental observations of Boo and Lee (1983) on interspecific crosses between *Antithamnion sparsum* from Korea and *A. defectum* from California are instructive in this regard. Boo and Lee found that gonimoblast development and release of carpospores occurred in the cross of *A. sparsum* (male) \times *A. defectum* (female), but not in the reciprocal cross of *A. sparsum* (female) \times *A. defectum* (male). Fertilization occurred in the second cross; the supporting cell cut off an auxiliary cell that enlarged normally, and the carpogonium cut off a connecting cell. The connecting cell, however, failed to fuse with the auxiliary cell, and further development ceased at this point.

In the Ceramiales an early fertilization leading to diploidization of the auxiliary cell and normal carposporophyte development is often followed by fertilizations of nearby carpogonia that fail to produce carposporophytes (Hommsand 1963). Again, a connecting cell or both an auxiliary cell and a connecting cell may have been cut off, but fusion between the two fails to take place. If it should take place, the carposporophyte probably would abort.

Red algae are referred to as either procarpal or nonprocarpal, depending on the position of the auxiliary cell in relation to the carpogonial branch. The term "procarpal" has a checkered history (Silva & Johansen 1986) but, in general, procarps are said to be present if auxiliary cells are borne on the same branch system in close proximity to the carpogonial branch, and absent if they are borne in separate, more remote branch systems. The procarpal condition has probably arisen de novo in conjunction with the evolution of connecting cells and auxiliary cells in the Ceramiales and Rhodymeniales. Clusters of filaments that are produced secondarily and bear both carpogonia and auxiliary cells are inherently procarpal in the families Gloiosiphoniaceae (in part), Endocodiaceae, and Tichocarpaceae (Kylin 1956), and perhaps, also in the Sphaerococcaceae and Phacelocarpaceae (Searles 1968; Sjöstedt 1926). *Callophyllis* and a few other genera belonging to the Kallymeniaceae have become procarpal secondarily through the loss of connecting filaments with the transfer of gonimoblast development to a fusion cell formed from part of the carpogonial branch apparatus (Norris 1957). In the Cystocloniaceae and Hypneaceae, families thought to be related to the Solieriaceae, the auxiliary cell is an inner cortical cell that is suprajacent to the supporting cell of the carpogonial branch (Min-Thein & Womersley 1976). The affinities of the procarpal families Mycho-deaceae, Acrotylaceae, Dicranemaceae, and Sarcodiaceae are thought to lie ultimately with the nonprocarpal family Solieriaceae or the procarpal family Cystocloniaceae (Kraft 1977b,c, 1978); the origin of procarps in the Plocamiaceae (Kylin 1928) and in the Gigartinaceae-Phyllophoraceae assemblage (Mikami 1965) are entirely unknown.

V. MORPHOLOGY OF THE CYSTOCARP

Structurally the cystocarp may be divided into three compartments: (1) the outer photosynthetic tissues, (2) the modified, nonphotosynthetic inner gametophytic tissues, and (3) the developing carposporophyte. The three compartments are readily dif-

ferentiated using classical fixation and hematoxylin staining techniques as applied by Oltmanns (1898) and Kylin (1914 and subsequent papers). We have obtained comparable results with material fixed in 8% to 10% formalin-seawater and stored in 5% formalin-seawater using a modification of Wittmann's (1965) aceto-iron-hematoxylin-chloral hydrate technique (Coomans 1986; Hommersand & Fredericq 1988).

The photosynthetic compartment consists of assimilatory filaments or unmodified cortical tissues of the vegetative system, plus any secondary photosynthetic tissues generated before or after fertilization. These latter may include secondary assimilatory filaments, involucre, nemathecia, or pericarps that contain functional chloroplasts. In most red algae a complex multilayered structure called a cuticle overlies the external tissues. Kugrens (1980) has suggested that the cuticle functions as a differentially permeable membrane that allows small molecules to pass through while retaining larger molecules produced by photosynthesis in the spermatangial branches of *Polysiphonia*. The same would hold for the female reproductive system. It is not required that the cuticle be a true membrane, only that it delay or restrain the outward diffusion of metabolites required for carposporophyte nutrition. Most cystocarps we have observed are provided with a cuticle, and ostiolate cystocarps generally have the ostiolar region sealed with a plug prior to carposporophyte maturation, or the ostiole is not formed until after the cystocarp matures.

The second compartment consists of specially modified gametophytic cells or tissues that lie in close proximity to the carpogonia or auxiliary cells, or are so situated that they are readily contacted by developing carposporophytes. Such cells and tissues usually stain deeply with hematoxylin, aniline blue, or other stains that exhibit a degree of specificity for proteins. Some have increased numbers of nuclei, or their nuclei and nucleoli may be enlarged, and they may contain amplified levels of DNA seen with DNA-specific fluorochromes, such as DAPI. Deeply staining tissues have been referred to as nutritive tissues in the past (Drew 1954; Kylin 1956). We distinguish between ordinary nutritive tissues, in which the cell contents are consumed in a single cycle of generative activity, and special nutritive tissues that appear to persist for longer periods during carposporophyte development providing renewable resources. We call this latter type a nutrient-processing center. It is always identifiable by the presence of large numbers of small nuclei, moderate numbers of enlarged

nuclei, or single enlarged, often giant nuclei per cell. Examples are given in Section X.

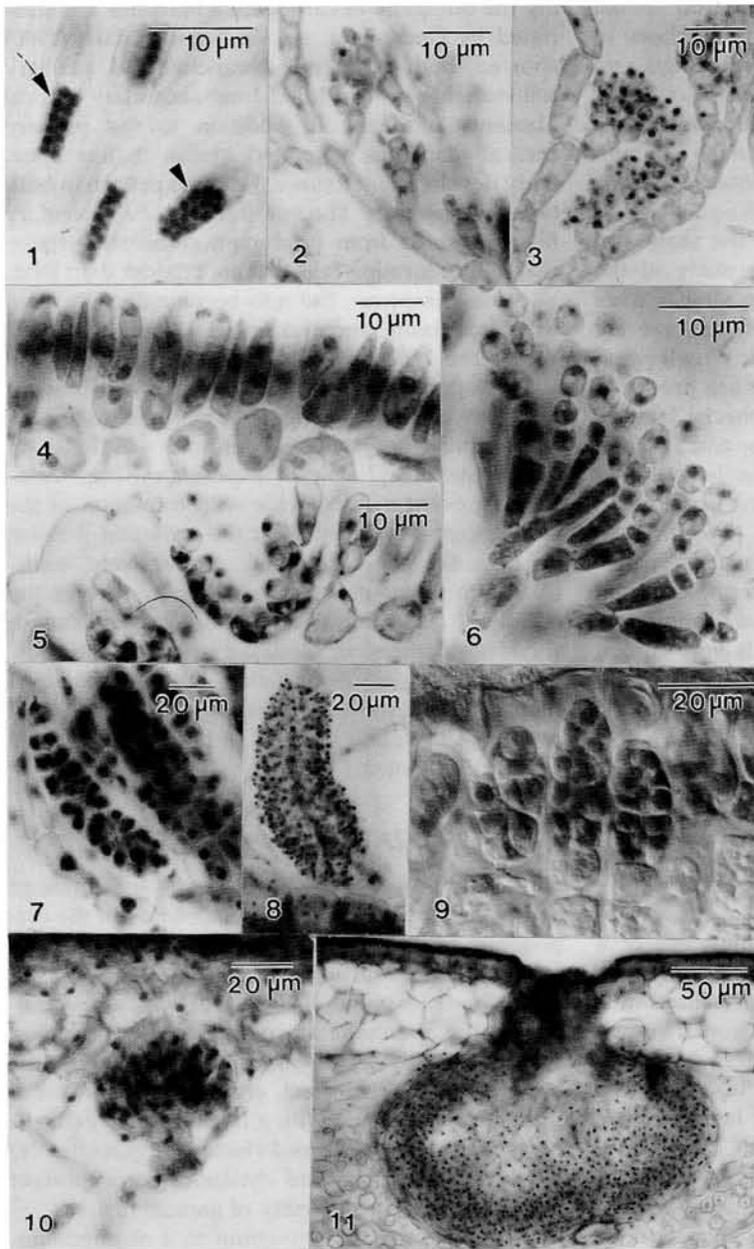
The third compartment is the carposporophyte itself which may consist of simple, unmodified filamentous gonimoblasts or be highly differentiated, sometimes with the production of auxiliary cells and connecting cells or connecting filaments. Morphological modifications of carposporophytic and closely associated gametophytic tissues may involve (1) enlargement and structural modification of existing pit connections, (2) fusions between contiguous cells either through or around the pit connections, sometimes with the formation of a central fusion cell, or (3) fusions or the production of secondary pit connections between gonimoblast cells and noncontiguous gametophytic cells, sometimes with formation of a well-defined placenta (see Sections X, XI).

VI. SPERMATANGIA AND SPERMATIA

Spermatogenesis follows a similar pattern in Bangiophycidae (Hawkes 1978), primitive Florideophycidae (Duckett & Peel 1978), and advanced Florideophycidae (Kugrens 1980; Scott & Dixon 1973). The condition of the nucleus is variable, with the chromatin ranging from dispersed to highly condensed. In the Corallinaceae the chromatin forms discrete cylindrical bodies aligned in two parallel plates (Fig. 13-1), suggesting that the nucleus is in arrested anaphase at the time of spermatial release (Duckett & Peel 1978). (The ultrastructure of spermatogenesis is described in Chapter 2.)

Spermatangia are borne separately in clusters of two to five on a spermatangial mother cell in the more primitive Florideophycidae (Figs. 13-2, 13-3). A single spermatium differentiates within each spermatangium. The spermatangial wall often remains after spermatial release, and new spermatia may proliferate within the older spermatangial walls (Scott & Dixon 1973). Spermatangia are generally initiated successively as subapical protrusions that are cut off by oblique septa in Florideophycidae (Dixon 1973). Initiation by transverse division is reported in *Gelidium* (Renfrew 1988) and occurs in some members of the Gracilariaceae (Fig. 13-4). In a few genera, such as *Holmsella* (Fig. 13-6) and *Endocladia* (Kylin 1956), the spermatangia are produced in linear rows.

The spermatangia of thalloid Florideophycidae commonly occur in superficial sori, as in *Gracilariopsis lemaneiformis* (Fig. 13-4). In *Gracilaria verrucosa* they are generated on branched filaments derived from a single initial and line the surface of a cavity



Figs. 13-1 to 13-11. Spermatangia and spermatangial branches [Unless otherwise indicated, all material was fixed in 5–8% Formalin-seawater and stained with aceto–iron–hematoxylin–chloral hydrate according to the method of Wittmann (1965) as modified by Coomans (1986) and Hommersand and Fredericq (1988).]
 13-1: *Metamastophora flabellata* (West Australia, material provided by W. Woelkerling), spermatangia with nuclei in anaphase in side view (arrow) and face view (arrowhead). 13-2: *Audouinella violacea* (North Carolina, material provided by R. Coomans). 13-3: *Dudresnaya crassa* (Florida). 13-4: *Gracilariopsis lemaneiformis* (California). 13-5: *Gracilaria verrucosa* (Ireland). 13-6: *Holmsella pachyderma* (Wales, material provided by E. Jones). 13-7, 13-8: *Polysiphonia harveyi* (North Carolina). 13-9: *Peyssonelia dubyi* (Ireland, material provided by C. Maggs). 13-10, 13-11: *Galaxaura diesingiana* (South Africa). (See text for descriptions.)

(Fig. 13-5). Spermatangia are produced on special spermatangial branches borne on trichoblasts in *Polysiphonia* (Fig. 13-7), with the spermatangia embedded in a confluent matrix beneath a common outer layer (Fig. 13-8). Spermatangial mother cells repeatedly proliferate spermatia within the common matrix, and older spermatia are released as young spermatia expand to take their place (Kugrens 1980).

In several families of red algae the male and female reproductive systems utilize many of the same developmental pathways. The similar male and female conceptacles of the Corallinaceae are a striking example (Johansen 1981; Woelkerling 1988). Spermatangia and carpogonia are produced in superficial pustules in the nemathelial families Rhizophyllidaceae, Peyssoneliaceae, and Polyidaceae. The spermatangia are borne laterally on spermatangial filaments formed during nemathelial development, as in *Peyssonnelia* (Fig. 13-9). In *Galaxaura* (Svedelius 1942) the male structure is produced from a modified filament bearing whorled laterals that resembles the carpogonial filament and forms an ostiolate conceptacle that is very similar to the female conceptacle (compare Figs. 13-10, 13-11 with Figs. 13-58, 13-59).

VII. THE CARPOGONIUM AND CARPOGONIAL BRANCH

Cell organelles do not appear to be modified extensively during carpogonial differentiation (See Chapter 2). In most Florideophycidae the carpogonium is transformed from the apical cell of a special lateral or terminal filament that usually contains a specified number of cells. Such a filament is called a carpogonial filament or carpogonial branch (Dixon 1973). Exceptions are the orders Acrochaetiales, Palmariales, and Gelidiales, in which the carpogonium is borne terminally or laterally on a vegetative filament or is intercalary (Gabrielson & Garbary 1986; Hommersand & Fredericq 1988).

A carpogonial branch can arise in one of two ways: (1) laterally, as a secondary filament produced by an adventitious initial, and (2) terminally, by transformation of the apical cell of an ordinary vegetative filament. In Ceramiales the carpogonial branch is almost always a four-celled filament developed from a lateral initial cut off from a periaxial cell (Hommersand 1963; Kylin 1923). In Liagoraceae it is either a lateral branch, as in most species of *Liagora*, or is terminal on a vegetative filament, as in *Nemalion* (Abbott 1976).

Some of the difficulties encountered in evaluat-

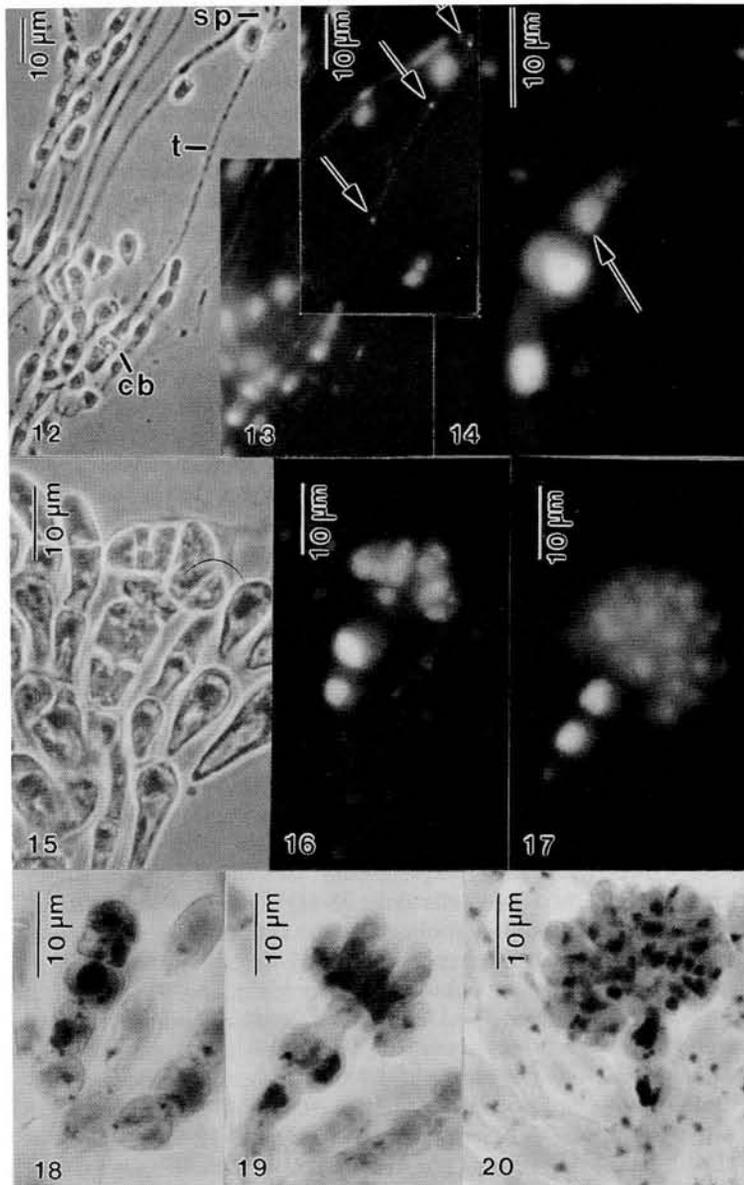
ing the ontogeny of carpogonial branches are illustrated by *Dudresnaya*. As Kraft and Robins (1985) showed, both carpogonial branches and auxiliary cell branches are modified from secondary cortical filaments produced in addition to the primary cortical filaments generated at the thallus apex. Early development follows the same pattern in both types of branches. The apical initial of a secondary filament shifts from producing elongated vegetative cells to forming cells that are broader than long. Vacuoles disappear, the cells become densely filled with cytoplasm, and the nuclei enlarge (Siotas & Wetherbee 1982).

Carpogonial branch (and auxiliary cell branch) ontogeny is probably triggered by genetically controlled processes that may or may not have an immediate morphological expression. The transforming event may coincide with formation of the carpogonial branch initial at the time that it is cut off from the supporting cell. Alternatively, transformation to a reproductive state may involve the apical cell of an already formed cortical filament, rhizoidal filament, or modified indeterminate axis. In this latter case delimitation of the carpogonial branch is determined by cytological changes, and filament length and position of the supporting cell are poorly defined.

VIII. FERTILIZATION

Fertilization in Rhodophyta is effected through spermatial adhesion to the surface layer of the carpogonial wall. Spermatia are thought to be transferred passively through the water column (Dixon 1973). In at least one instance, *Tiffaniella* (Ceramiales), the spermatia are released from a number of spermatangial heads into spermatial strands that coalesce, extend, contract, and rotate in the water until contact is made with a female plant (Fetter & Neushul 1981). Sheath and Hambrook (Chapter 16) have proposed that fluid dynamics are important in increasing the probability of gamete fusion.

Attachment of a spermatium to a carpogonium appears to require the presence of binding substances secreted by exocytosis from the tip of the trichogyne (Broadwater & Scott 1982). The binding between gametes of *Callithamnion* are not species specific, but occur only between closely related species (Magruder 1984). Trichogynes persist after fertilization in many Florideophycidae, and several spermatia may attach either near the tip of the trichogyne, as in *Batrachospermum* (Fig. 13-42), *Nemalion* (Fig. 13-12) or *Polysiphonia*, (Fig. 13-30), or along



Figs. 13-12 to 13-17. *Nemalion helminthoides* (California, phase contrast and ultraviolet photographs by M. Rosczyk from material stained with DAPI). 13-12: Carpogonial branch (cb) and trichogyne (t) with attached spermatia (sp) in phase contrast. 13-13: Sperm nuclei (arrows) within trichogyne (UV). 13-14: Sperm nucleus (arrow) fused to egg nucleus (UV). (Note enlarged nuclei in hypogynous and subhypogynous cells). 13-15: Carpogonial branch with gonimoblasts (phase). 13-16: Same as Fig. 13-15 (UV). 13-17: Older gonimoblasts (UV).
 Figs. 13-18 to 13-20. *Nemalion helminthoides* (Nova Scotia), stages of carpogonial branch fusion and gonimoblast development.

its sides, as in *Acrosymphyton* (Figs. 13-80, 13-81). We have observed that in some genera, such as *Gelidium* and *Gracilaria*, the trichogyne collapses soon after fertilization, and attached spermatia are rarely seen.

Spermatia may first attach to vegetative cells. In *Callithamnion*, the spermatia have fimbriate, cone-shaped appendages projecting from both ends that are visible with scanning electron microscopy (Magruder 1984). These may attach initially to vegetative hair cells and later bind to a nearby trichogyne. In *Hymenena* (Delesseriaceae) spermatia appear to attach to the thallus surface. Trichogynes of receptive carpogonia, which just break the thallus surface, appear to extend toward the spermatium and fuse with it (Hommersand, unpubl.). It is possible that the spermatia of some species secrete a chemotropic substance that promotes the directed growth of the trichogyne.

Breakdown of the carpogonial wall and entry of the spermatium nucleus and cytoplasm appear to involve the enzymatic digestion of the wall. In *Porphyra* a narrow channel, the fertilization canal, is formed, through which the spermatial nucleus passes (Hawkes 1978). The fusion area is broader in other red algae and leads to an open connection between the cytoplasm of the spermatium and that of the carpogonium. Several nuclei from different spermatia may enter the carpogonium in *Porphyra*, although only one appears to fuse with the carpogonial nucleus (Hawkes 1978). With the exception of the Batrachospermales, the trichogyne of Florideophycidae has a narrow neck at its base that admits the passage of a single nucleus. In *Polysiphonia* (and probably most other Florideophycidae) the vacuole contracts immediately after the sperm nucleus has entered the base of the carpogonium and draws the sperm nucleus into contact with the egg nucleus, at the same time pinching off the cytoplasm (Broadwater & Scott 1982). The latter event separates the trichogyne from the inflated base of the carpogonium, effectively preventing super-numerary fertilizations.

IX. PRODUCTS OF THE FERTILIZATION NUCLEUS

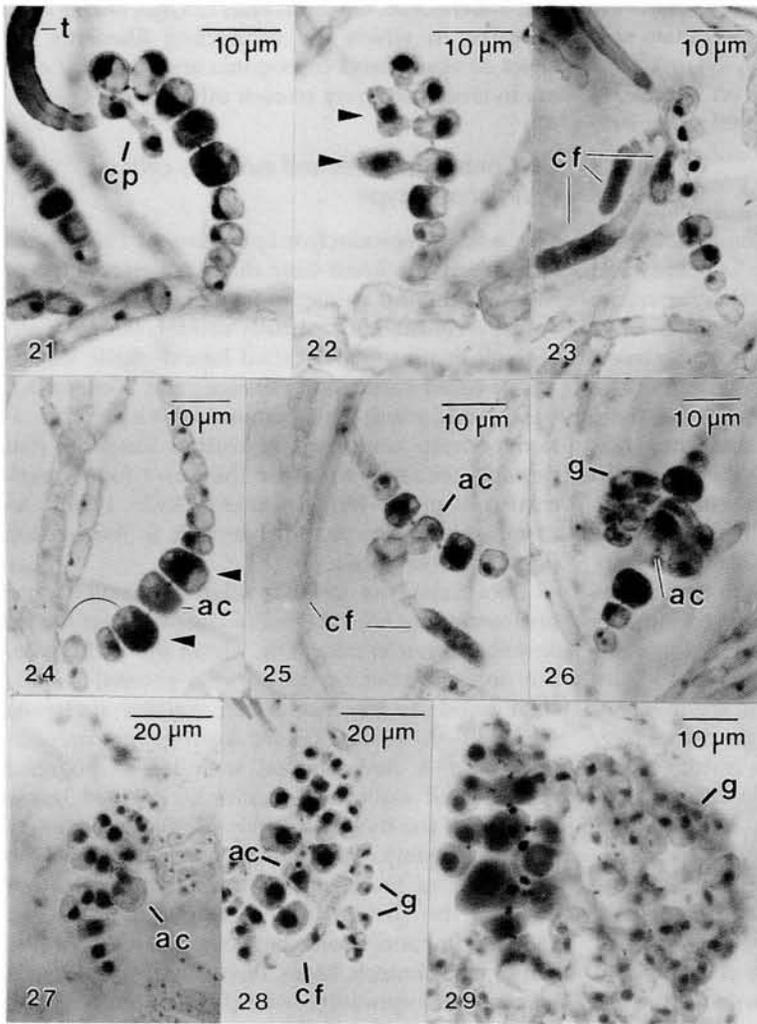
We recognize three major patterns of carposporophyte development based on the fate of the first cell derivatives cut off from the carpogonium that carry the division products of the fertilization nucleus: (1) they give rise directly to gonimoblasts (*Nemalion* type), (2) they initiate connecting processes or fila-

ments that unite with one or more auxiliary cells, and either the gonimoblasts develop directly from the connecting filament or a diploid nucleus is transferred to the auxiliary cell, which produces the gonimoblasts (*Dudresnaya* type), or (3) they cut off one, two, or three connecting cells, each of which may fuse with an adjacent auxiliary cell, depositing its nucleus, and the auxiliary cell produces the gonimoblasts (*Polysiphonia* type).

A. Direct formation of gonimoblasts: *Nemalion* type

The following report of carposporophyte development in *Nemalion* is based primarily on the research of Rosczyk (1984). The carpogonium of *Nemalion* is borne terminally on a lateral filament that is not at first distinguishable from a vegetative lateral. At about the same time that the carpogonium initiates a trichogyne, the hypogynous cell and the cell immediately below it expand and their nuclei enlarge. Staining with DAPI reveals that the DNA levels of these nuclei become greatly amplified during differentiation of the carpogonial branch prior to fertilization (Rosczyk 1984). Several spermatia may become attached near the tip of the trichogyne (Fig. 13-12) and sperm nuclei can be seen migrating through the trichogyne towards the carpogonium (Fig. 13-13). Usually, only one sperm nucleus unites with the carpogonial nucleus (Fig. 13-14). The fertilized carpogonium first divides transversely into two cells (Fig. 13-18). Only the terminal cell produces gonimoblasts, while the lower cell fuses with the hypogynous and subhypogynous cells of the carpogonial branch containing the enlarged nuclei (Fig. 13-19). The modified nuclei of these cells persist within the fusion cell throughout the course of gonimoblast development and are conspicuous when stained either with DAPI (Figs. 13-15 to 13-17) or hematoxylin (Figs. 13-19, 13-20). Branching of the carposporophyte is initially monopodial, with the terminal gonimoblast cells differentiating into carposporangia (Fig. 13-19). Once carposporangia have formed, lateral filaments are initiated from subterminal cells, and there is a shift to a pattern of sympodial growth as terminal cells differentiate successively into carposporangia (Ramm-Anderson & Wetherbee 1982).

Direct development of gonimoblasts from the carpogonium is seen in the orders Acrochaetales, Batrachospermales, Nemaliales, Gelidiales, and Bonnemaisoniales, and in *Ahnfeltia* and the family Gracilariaceae, as described in Section X.



Figs. 13-21 to 13-26. *Dudresnaya crassa* (Florida). 13-21: Division of fertilized carpogonium (cp) with trichogyne (t). 13-22: Fusion of carpogonium and its derivative cell (arrowheads). 13-23: Fusion cells issuing connecting filaments (cf). 13-24: Auxiliary cell filament, auxiliary cell (ac) and adjoining nutritive cells (arrowheads). 13-25: Connecting filament (cf) fused to auxiliary cell (ac). 13-26: Auxiliary cell (ac) bearing gonimoblasts (g).

Figs. 13-27 to 13-29. *Kraetia dichotoma* (South Australia, photographs by M. Knauss). 13-27: Auxiliary cell branch and auxiliary cell (ac). 13-28: Auxiliary cell (ac), connecting filament (cf) and gonimoblasts (g). 13-29: Auxiliary cell branch with modified pit connections and gonimoblasts (g).

B. Connecting filaments and auxiliary cells: *Dudresnaya* type

Dudresnaya is a comparatively primitive member of the family Dumontiaceae (Gigartinales). The details of postfertilization development have been particularly well documented by Robins and Kraft (1985).

Cells of the carpogonial filament become differentiated before fertilization and contain enlarged nuclei, especially the fourth and fifth and sometimes the sixth cells behind the carpogonium. Typically, the carpogonium elongates alongside the carpogonial filament after fertilization (Fig. 13-21) and cuts off a derivative cell. The carpogonium and its derivative

fuse with the fourth and fifth cells, respectively (Fig. 13-22). The resulting fusion cells initiate several connecting filaments (Fig. 13-23).

The auxiliary cell in *Dudresnaya* is an intercalary cell in a separate filament that is homologous with the carpogonial branch. It is easily distinguished in hematoxylin-stained material by the presence of an unmodified nucleus containing a nucleolus surrounded by a clear hyaline region (Fig. 13-24). The cells on either side of the auxiliary cell are enlarged and contain highly modified, deeply staining nuclei (Fig. 13-24). When a connecting filament reaches the vicinity of an auxiliary cell, it cuts off an intercalary segment by two successive divisions. The auxiliary cell and the intercalary segment fuse, while the terminal cell remains a connecting filament (Fig. 13-25). An auxiliary cell that is not in close proximity to the intercalary segment will form a process that extends toward and fuses with the segment of the connecting filament. The intercalary segment may branch, cutting off one to two initials that develop into secondary connecting filaments (Robins & Kraft 1985). Ultimately, two to three gonimoblasts are produced from the segment of the connecting filament that has fused to the auxiliary cell, and these coalesce to form a single cluster (Fig. 13-26). Pit connections between the nutritive cells of the auxiliary cell branch increase in surface area, often becoming convoluted (Siotas & Wetherbee 1982).

Kraftia is similar to *Dudresnaya* except that the auxiliary cell filament is branched and contains a greater number of modified cells with enlarged nuclei (Fig. 13-27). The nuclei in the cells adjacent to the auxiliary cell continue to enlarge during gonimoblast development, and the pit plugs broaden asymmetrically, becoming broader on the side facing toward the auxiliary cell (Figs. 13-28, 13-29). Connecting filament behavior and gonimoblast development follow a common pattern in most genera of Dumontiaceae (Lindstrom & Scagel 1987).

Connecting filaments occur only in the orders Cryptonemiales and Gigartinales, as illustrated in Section X. The connecting filaments are septate and frequently branched in the families Calosiphoniaceae, Nemastomataceae, Furcellariaceae, Acrosymphytaceae, Polyideaceae, Rhizophyllidaceae, and Peyssonneliaceae. They are essentially non-septate and form secondary connecting filaments in the vicinity of auxiliary cells in the Dumontiaceae, Gloiosiphoniaceae, Halymeniaceae, and most Kallymeniaceae. Alternatively, connecting filaments may be unbranched and terminate with the diploidization of a single auxiliary cell in the Caulacanthaceae

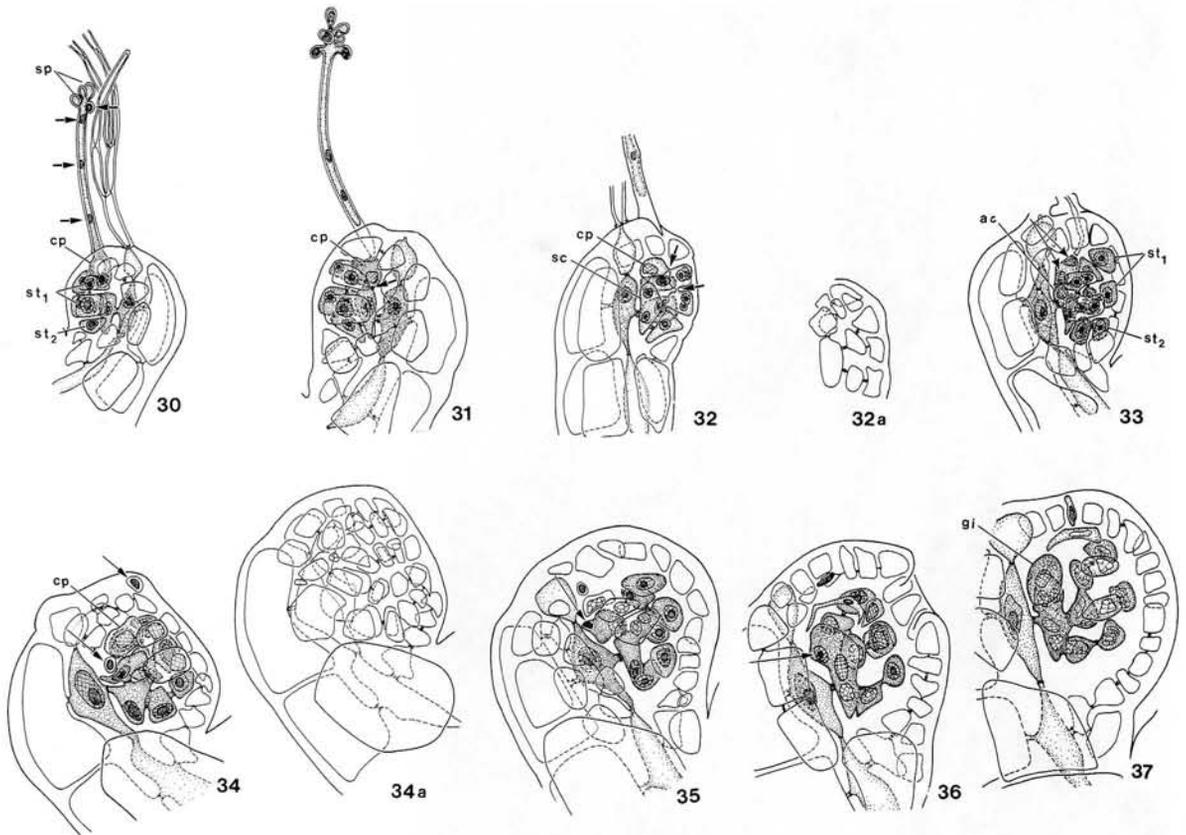
and Solieriaceae. Other families of Gigartinales have procarps in which the connecting filaments are short or absent and carpogonia and auxiliary cells are in close proximity to each other.

C. Connecting cells and auxiliary cells: *Polysiphonia* type

The female reproductive apparatus of *Polysiphonia* is regularly produced from the fifth periaxial cell of the second-basal segment of a modified trichoblast. Before fertilization it normally consists of a supporting cell bearing a two-celled lateral sterile group, a four-celled carpogonial branch, and a one-celled basal sterile group. It is surrounded by a prefertilization pericarp composed of cortical filaments that develop primarily from the third and fourth periaxial cells of the fertile segment (Kylin 1956). Occasionally, the carpogonial branch is three-celled (Figs. 13-30 to 13-37).

The trichogyne persists after fertilization, and one commonly sees spermatia attached near the tip and sperm nuclei migrating within the trichogyne. The total number of male nuclei present usually corresponds to the number of attached spermatia (Figs. 13-30, 13-31). Before karyogamy, the carpogonium is flask shaped with the carpogonial nucleus and associated vacuole suspended below the base of the trichogyne (Fig. 13-30). Immediately after karyogamy, the trichogyne separates and the carpogonium broadens and forms a process that contacts the surface of the supporting cell (Fig. 13-31). Pit connections between the cells of the carpogonial branch break down, and the nucleus inside the supporting cell divides (Fig. 13-32). Broadwater and Scott (1982) documented this stage with electron microscopy and suggested that a hormone released from the fertilized carpogonium is transported through the carpogonial branch to the supporting cell, where it triggers formation of the auxiliary cell.

The carpogonium next divides (Fig. 13-33), cutting off the first connecting cell toward the outside, which is nonfunctional. The second division of the zygote nucleus produces a connecting cell along the inner side of the auxiliary cell (Fig. 13-34). The auxiliary cell then expands and fuses with the connecting cell (Fig. 13-35). Contrary to reports in the literature (Broadwater & Scott 1982; Kylin 1923), we have never seen evidence of direct fusion between the auxiliary cell and the carpogonium that resulted in the transfer of a derivative of the fertilization nucleus. Concomitant with these events, terminal cells of the pericarp filaments are converted into



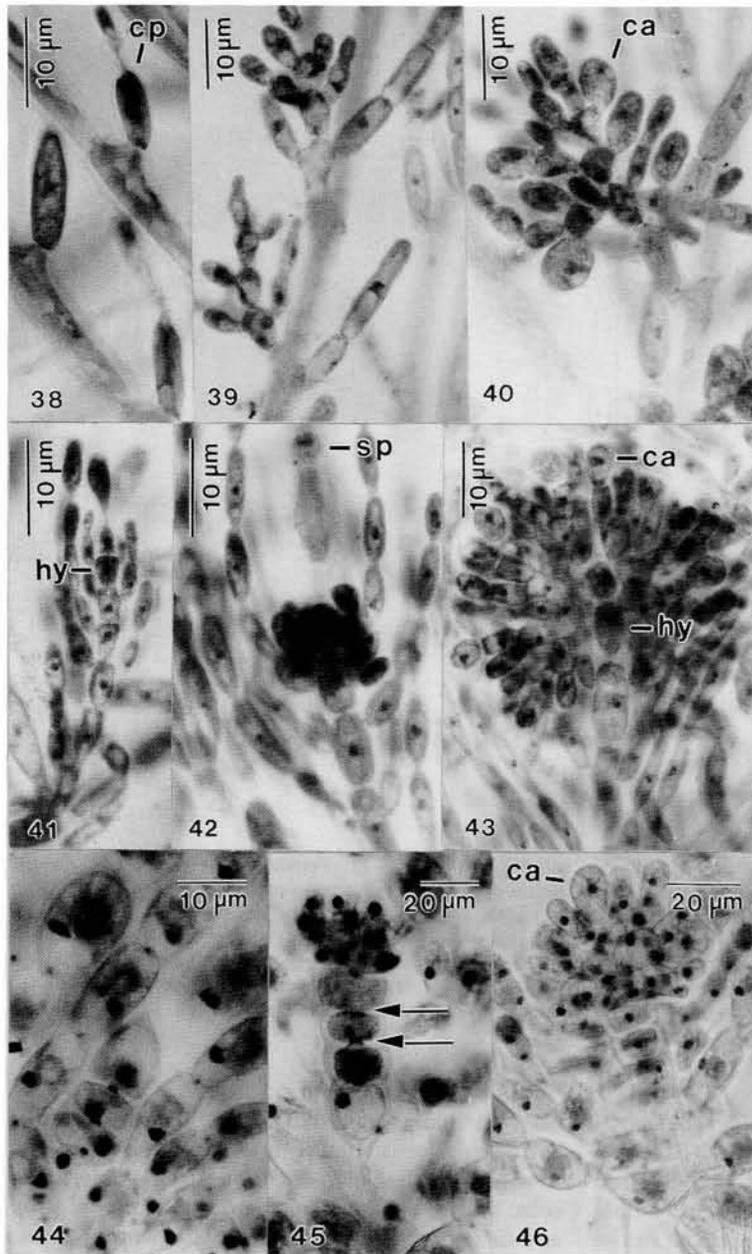
Figs. 13-30 to 13-37. *Polysiphonia harveyi* (North Carolina). 13-30: Fertilized carpogonium (cp) before karyogamy showing spermatia (sp) and sperm nuclei (small arrows), with two-celled sterile group 1 (st₁) and one-celled sterile group 2 (st₂). 13-31: Carpogonium (cp) after karyogamy contacting supporting cell (small arrow). 13-32: Supporting cell (sc) after nuclear division; pit connections between cells of carpogonial branch have degenerated (small arrows). 13-32a: Pericarp

of Fig. 13-32. 13-33: Fertilization nucleus has divided (arrows), auxiliary cell (ac) cut off, sterile groups 1 and 2 (st₁, st₂) have divided. Fig. 13-34: Carpogonium (cp) has cut off two connecting cells (arrows). 13-34a: Pericarp of Fig. 13-34. 13-35: Auxiliary cell fused with inner connecting cell (arrow). 13-36: Diploid nucleus (arrow) expanded inside auxiliary cell. 13-37: Gonimoblast initial (gi).

apical initials of axial files that produce the post-fertilization pericarp (compare Figs. 13-32a and 13-34a), and the two sterile groups divide once, so that sterile group 1 becomes four-celled and sterile group 2 becomes two-celled (Fig. 13-33). The nuclei within cells of each of the two sterile groups enlarge and stain deeply with hematoxylin. Pit connections break down between the sterile groups and the supporting cell (Figs. 13-35, 13-36), followed by dissolution of the pit connections between the outer and inner cells of the sterile groups themselves (Fig. 13-37). The diploid nucleus inside the auxiliary cell enlarges (Fig. 13-36) and divides, cutting off the gonimoblast initial (Fig. 13-37), which remains quiescent while the photosynthetic pericarp expands to its full size. Branching of the gonimo-

blast is initially monopodial but becomes sympodial as terminal cells mature into carposporangia and new gonimoblast filaments issue from subterminal cells. The gonimoblast initial and auxiliary cell fuse, and fusions extend progressively to incorporate the inner cells of the gonimoblast. Nuclei and proplastids break down inside the expanding fusion cell, and pit connections between unfused gonimoblast cells lose their cap membranes (Wetherbee 1980).

A derivative of the zygote nucleus is transferred to the auxiliary cell either by a carpogonial process or through direct fusion, or transfer is mediated by a connecting cell in Ceramiales and Rhodymeniales (Dixon 1973). Connecting cells are well documented in the family Dasycyaceae (Parsons 1975). Our own



Figs. 13-38 to 13-40. *Audouinella violacea* (North Carolina, material provided by R. Coomans). 13-38: Unfertilized carpogonia (cp). 13-39, 13-40: Developing gonimoblasts with young carposporangia (ca).

Figs. 13-41 to 13-43. *Batrachospermum boryanum* (North Carolina, material provided by R. Coomans). 13-41: Carpogonial branch with deeply staining hypogynous cell (hy). 13-42: Fertilized carpogonium with attached spermatium (sp) and gonimoblasts. 13-43: Gonimoblasts with terminal carposporangia (ca) and deeply staining hypogynous cell (hy).

Figs. 13-44 to 13-46. *Liagora mucosa* (Florida). 13-44: Lateral carpogonial branch. 13-45, 13-46: Carpogonial branch with broadened pit connections (arrows), developing gonimoblasts, and terminal carposporangia (ca).

survey indicates that direct transfer occurs in the Antithamniaeae, Ptiloteae, and Ceramieae, but that diploidization of the auxiliary cell is effected by means of a connecting cell in most other tribes of Ceramiaceae and in the families Delesseriaceae, Dasyaceae, and Rhodomelaceae. Connecting cells have been illustrated for the Rhodymeniaceae (Sparling 1957) and the Champiaceae (Bliding 1928) of the Rhodymeniales, and direct fusions have also been reported between the fused carpogonial branch and the auxiliary cell (Lee 1978).

X. FUNCTIONAL ADAPTATIONS OF CYSTOCARP MORPHOLOGY

A. Absence of special nutritive tissues: Acrochaetiales and Palmariales

Among the Florideophycidae only the Acrochaetiales and Palmariales appear to lack supplementary vegetative nutritive filaments or specially modified vegetative cells. In most Acrochaetiaceae the carpogonium divides transversely after fertilization, and both the upper and lower cells produce gonimoblasts (Woelkerling 1970). A comparison of female thalli of *Audouinella violacea* before and after fertilization (Figs. 13-38 to 13-40) shows little evidence of the production of secondary assimilatory filaments and no obvious cytological differentiation of vegetative cells. Moreover, pit connections between adjoining cells do not seem to enlarge or become modified. In *Palmaria* the fertilized carpogonium gives rise directly to a free-living sporophyte that develops autotrophically (van der Meer & Todd 1980).

B. Modified carpogonial branches: Batrachospermales and Nemiales

The Batrachospermales comprises an independent line in which the nutritive system is relatively unspecialized in most species of *Batrachospermum* (Batrachospermaceae) but is highly modified in *Lemanea* (Lemaneaceae). Carpogonia are terminal on cortical filaments or on modified indeterminate branches in *Batrachospermum boryanum*. The hypogynous cell is deeply staining, and inner cells of the carpogonial branch bear juvenile filaments before fertilization (Fig. 13-41) that grow into functional assimilatory filaments as the carposporophyte develops (Figs. 13-42 to 13-43). A spermatium often persists, attached to the fertilized carpogonium (Fig. 13-42), and the carpogonium gives rise directly

to gonimoblasts bearing terminal carposporangia (Fig. 13-43). Although pit connections between cells of the carpogonial branch and inner gonimoblast cells enlarge somewhat, they are only slightly modified (Kylin 1917). An extensive fusion cell is formed in *Tuomeya* (Webster 1958).

The female reproductive system of the Lemaneaceae is highly specialized. Carpogonial branches of *Lemanea* are restricted to internodal regions and are four to ten cells long. As they mature, the plasters degenerate, and spherical-celled laterals develop profusely from all cells of the carpogonial branch except the carpogonium (Mullahy 1952a). After fertilization, the sterile laterals increase in number and become deeply staining with hematoxylin. Gonimoblasts originate directly from the carpogonium and overgrow and penetrate among the sterile laterals. Subsequently, inner gonimoblast cells fuse, rupturing their pit connections, while the sterile laterals become vacuolate (Mullahy 1952b). Outer gonimoblast filaments are unpigmented and profusely branched, with most of the cells maturing into chains of carposporangia.

The multiaxial family Thoreaceae is presently placed in the Batrachospermales (Yoshizaki 1986). Recent studies have demonstrated that the carposporophyte develops directly from the carpogonium in *Thorea* and ramifies among the surrounding gametophytic filaments (Necchi 1987; Yoshizaki 1986). No specialized vegetative cells or filaments have been described, and cell fusions appear to be absent.

The multiaxial order Nemiales contains at least two families, the Liagoraceae and Galaxauraceae. Secondary assimilatory filaments are produced directly on the carpogonial branch or are formed by cortical filaments in the immediate vicinity of a fertilized carpogonium. Only cells of the carpogonial branch or laterals borne on it may contain modified nuclei. Basic features of sexual reproduction in Nemiales were described for *Nemalion helminthoides* in Section IX.A.

Carpogonial branches are lateral in *Liagora mucosa* (Fig. 13-44). The carpogonium divides transversely after fertilization, with only the distal cell producing gonimoblasts (Fig. 13-45). Cortical cells adjacent to the supporting cell characteristically produce secondary assimilatory filaments that coalesce to form an involucre surrounding the carposporophyte. The cells of the carpogonial branch are little modified during carposporophyte development. Nuclei remain small, and pit connections between adjacent cells broaden slightly (Figs. 13-45, 13-46). Cell fusions appear to be absent.

Gonimoblast filaments ramify among the surrounding assimilatory filaments in *Dermonema frapieri* without fusing with them (Svedelius 1939). The supporting cell and cells of the carpogonial branch contain enlarged nuclei and stain heavily for protein before fertilization (Fig. 13-47). They retain their modified nuclei and staining properties during gonimoblast development (Fig. 13-48) and eventually unite into a fusion cell (Fig. 13-49).

An undescribed species of *Trichogloea* possesses several unusual characters. Assimilatory filaments are absent from the carpogonial filament before fertilization (Fig. 13-50) and are only produced after fertilization (Figs. 13-51, 13-52). The unfertilized carpogonium stains deeply and contains two nuclei: an egg nucleus with a typical nucleolus and an enlarged, modified nucleus (Fig. 13-50). Cells of the carpogonial branch fuse around the primary pit connections after fertilization, and the fusion cell becomes multinucleate and rich in protein content (Fig. 13-51). Later, it becomes vacuolate, and the remnant primary pit connections can be seen (Fig. 13-52). Ultimately, fusions extend to include the basal cells of the gonimoblast (Fig. 13-53) and, as was described for *Nemalion*, branching is initially monopodial, becoming sympodial as the terminal cells mature into carposporangia (Fig. 13-54).

Some of the trends seen in the Liagoraceae are carried further in the Galaxauraceae. In both *Scinaia* and *Galaxaura* the carpogonium is the terminal cell of a three-celled fertile branch in which both the hypogynous cell and the basal cell bear lateral filaments (Svedelius 1915, 1942). In *Scinaia* the hypogynous cell and its laterals are enlarged, stain deeply, and contain greatly enlarged nuclei, and the basal cell bears a whorl of juvenile involucre filaments (Fig. 13-55). An extensive involucre develops after fertilization while the nuclei in the hypogynous cell and its laterals persist (Fig. 13-56). The carpogonium produces four gonimoblast initials that fuse inwardly with the carpogonium, the hypogynous cell, and its laterals and outwardly with the inner sterile cells of the gonimoblast (Fig. 13-57).

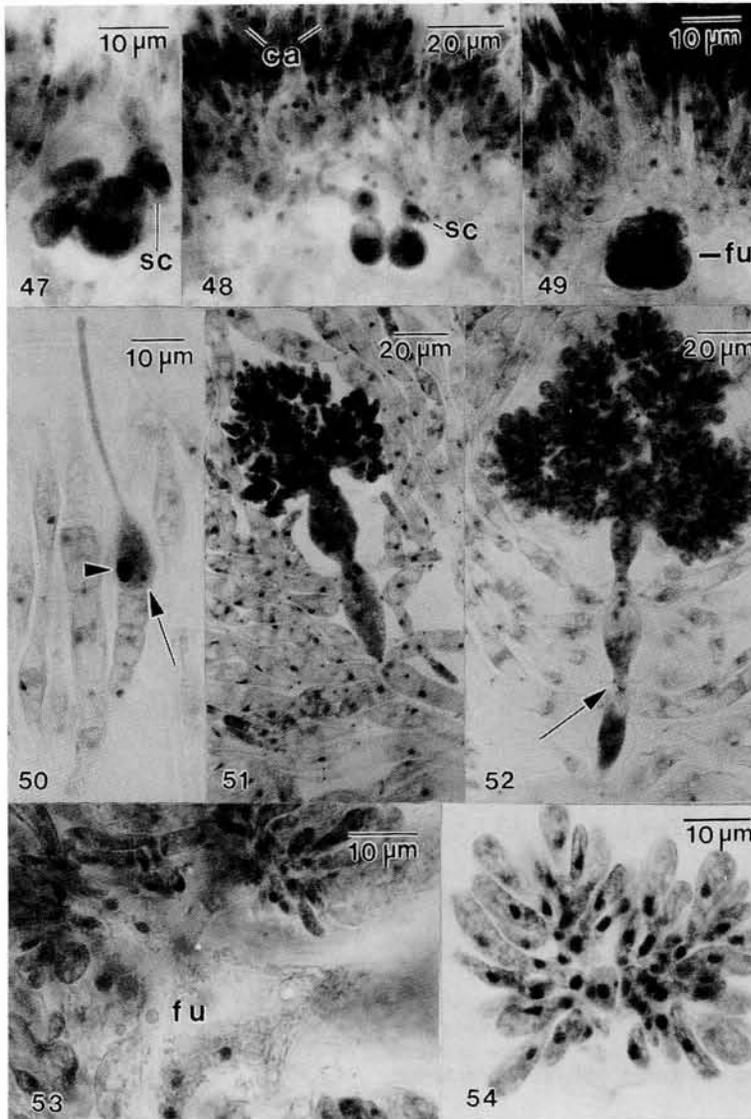
The lateral filaments borne on the hypogynous cell are extensively branched in *Galaxaura*, and each cell contains an enlarged nucleus, whereas the involucre filaments are only weakly developed on the basal cell prior to fertilization (Fig. 13-58). Fusions become even more extensive after fertilization than in *Scinaia* and incorporate a much larger portion of the enveloping involucre system (Figs. 13-59, 13-60). Filaments of the carposporophyte branch in close association with the developing involucre to form a conceptacle with an ostiole.

C. The female conceptacle and fusion cell: Corallinales

Several theories have been proposed to account for the structure of the female reproductive system in the Corallinales (Lebednik 1977; Woelkerling 1980), but postfertilization events are not fully understood. Woelkerling (1980) observed in *Metamastophora* that a channel forms between the fertilized carpogonium and the supporting cell as a result of direct fusion through the hypogynous cell. Multiple fertilizations may take place, resulting in the formation of several initial fusion cells in *Synarthrophyton* (Woelkerling & Foster 1989). The initial fusion appears to extend laterally through the floor of the conceptacle at the level of the supporting cells of the carpogonial branches to form a plate-like fusion cell characteristic of many Corallinales (Johansen 1981; Woelkerling 1988). Gonimoblast filaments bearing terminal carposporangia are produced at the margin of the fusion cell in *Metamastophora flabellata* (Figs. 13-61, 13-62). In *Metamastophora* the haploid nucleus of each supporting cell remains in a fixed position within the fusion cell, where it enlarges (Figs. 13-62, 13-63). Clavate paraphyses situated adjacent to carpogonial branches persist on each supporting cell after fertilization and develop enlarged nuclei and conspicuous globules (Fig. 13-62). Pit plugs between the fusion cell and the gonimoblast filaments broaden and thicken, and dome-shaped plug caps form over the pit connections between the paraphyses and the fusion cell (Fig. 13-63) and between the gonimoblast filaments and fusion cell (Fig. 13-64). The conceptacle of Corallinales appears to be similar functionally to the cystocarp of other red algae, with the outer cortex serving as the photosynthetic compartment and the fusion cell acting as a nutrient-processing center.

D. Preformed nutritive tissues: Gelidiales

The nutritive system is largely formed before fertilization in the Gelidiales (Fan 1961; Hommersand & Fredericq 1988). Deeply staining, branched nutritive filaments are produced secondarily from inner cortical cells at the tips of fertile female pinnules prior to carpogonium maturation. Nuclei in the cortical cells adjacent to the carpogonium enlarge after fertilization, and a channel develops through the pit connections leading to the carpogonium in *Gelidium pteridifolium* (Hommersand & Fredericq 1988). At the same time that the carpogonium fuses with the adjoining cortical cells it becomes multinucleate and initiates uninucleate gonimoblast fila-

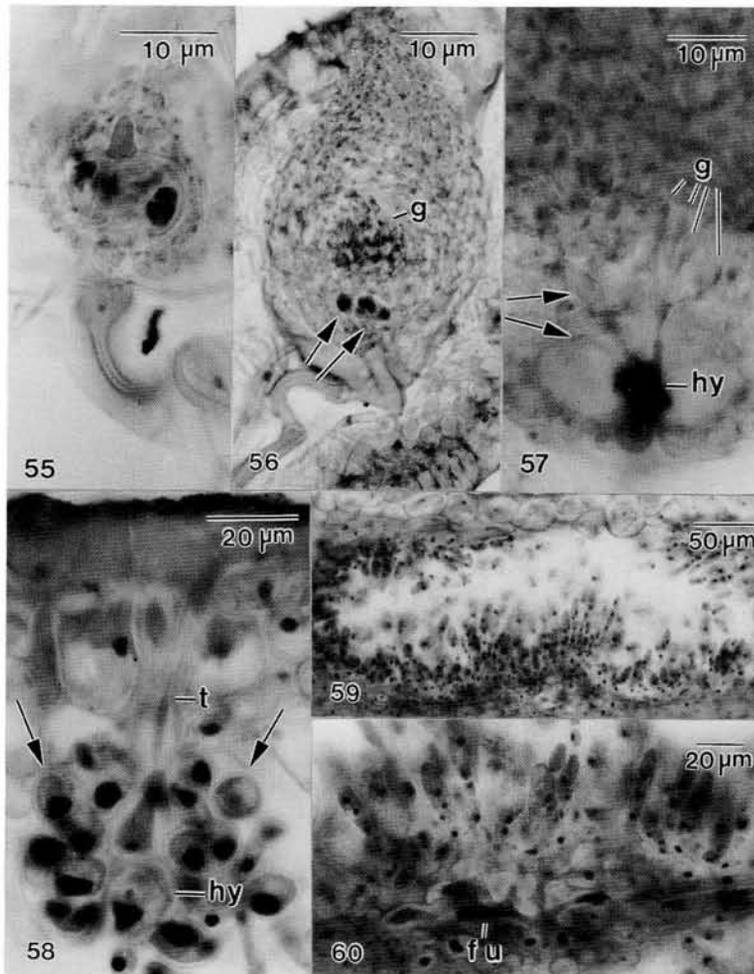


Figs. 13-47 to 13-49. *Dermonema frappieri* (Taiwan, material collected by S. Martinique). 13-47: Supporting cell (sc) and carpogonial branch. 13-48, 13-49: Supporting cell (sc), developing fusion cell (fu) and gonimoblasts with terminal carposporangia (ca).

Figs. 13-50 to 13-54. *Trichogloea* sp. (Virgin Islands, material provided by J. Sears). 13-50: Carpogonium with egg nucleus (arrow) and modified nucleus (arrowhead). 13-51: Fused, multinucleate carpogonial branch with developing gonimoblasts and assimilatory filaments. 13-52: Fusions around pit connection (arrow). 13-53: Gonimoblast fusion cell (fu). 13-54: Sympodially branched gonimoblast.

ments that ramify among the clusters of nutritive filaments in both *Gelidium* (Fig. 13-65) and *Suhria* (Fig. 13-66). Terminal gonimoblast cells either fuse specifically with the terminal cells of nutritive filaments, as in *G. pteridifolium* (Fig. 13-67), or ran-

domly with terminal and intercalary cells, as in *S. vittata* (Figs. 13-68, 13-69), before cutting off carposporangial initials. At maturity the cystocarp is biconvex in *Gelidium* and *Suhria* and consists of a central partition supporting a plexus of intercon-



Figs. 13-55 to 13-57. *Scinia complanata* (North Carolina, material collected by G. Hansen). 13-55: Mature unfertilized carpogonial branch. 13-56: Developing gonimoblasts (g), hypogynous cell, and its laterals (arrows) surrounded by involucreal filaments. 13-57: Gonimoblasts (g) fused to hypogynous cell (hy) and its laterals (arrows).

Figs. 13-58 to 13-60. *Galaxaura diesingiana* (South Africa). 13-58: Carpogonial branch with carpogonium, trichogyne (t) and hypogynous cell (hy) bearing modified lateral filaments with enlarged nuclei. 13-59: Cross section of cystocarp. 13-60: Fusion cell (fu) at base of cystocarp.

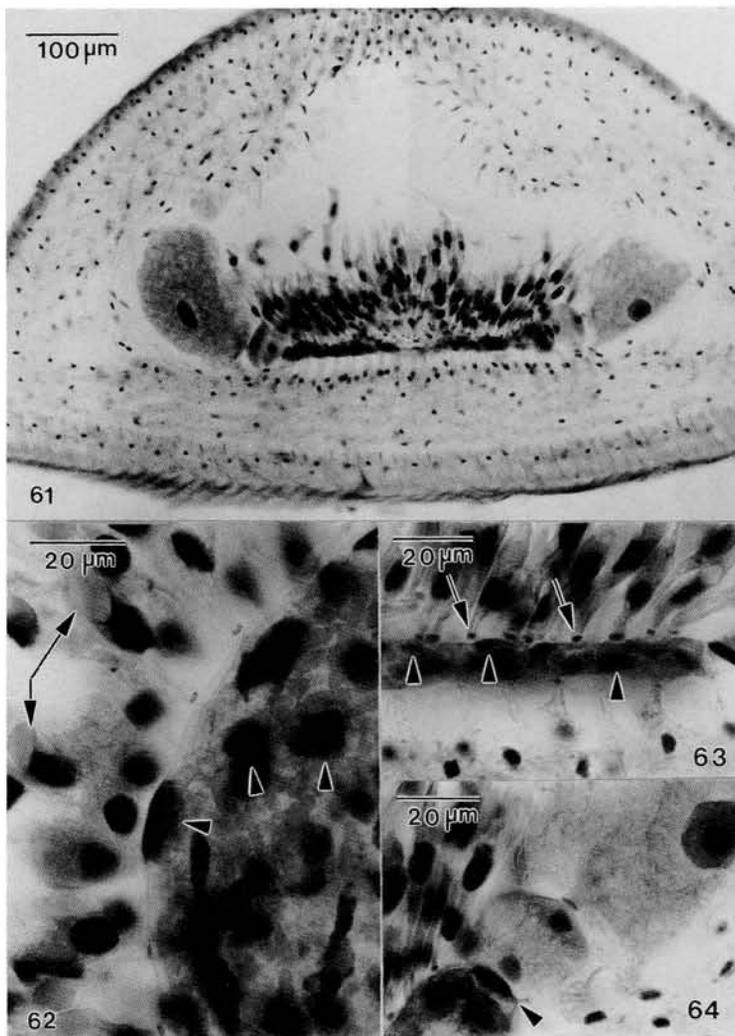
nected nutritive and gonimoblast filaments bearing carposporangia, surmounted by pericarps transformed from slightly modified cortex on either side (Fig. 13-70).

E. Preformed nutritive tissues: Gigartinales

The primitive type of sexual reproduction in the Gigartinales is thought to be one in which the carpogonia and auxiliary cells are borne in separate

branch systems (nonprocarpial) and many connecting filaments issue from a single fertilized carpogonium and give rise directly to gonimoblasts after uniting with auxiliary cells (Drew 1954; Kraft 1981). This type is represented by the genus *Dudresnaya* (Dumontiaceae), described in Section IX.B, and by representatives of the Calosiphoniaceae, Nemastomataceae, and several advanced families.

In *Schmitzia hiscockiana* (Calosiphoniaceae) the carpogonial branch is a three-celled lateral filament

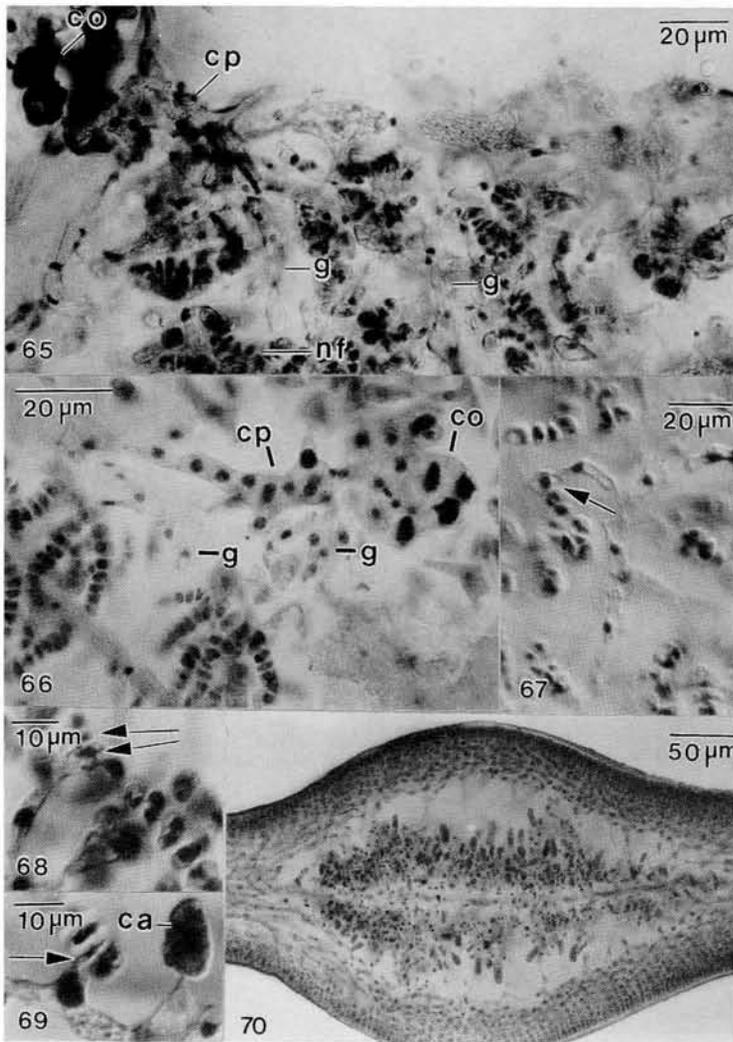


Figs. 13-61 to 13-64. *Metamastophora flabellata* (Western Australia, alcohol preserved material provided by W. Woelkerling). 13-61: Cross section of mature cystocarpic conceptacle. 13-62: Fusion cell with enlarged nuclei (arrowheads) and paraphyses with enlarged nuclei and globular bodies (arrows) in surface view. 13-63: Fusion cell with enlarged nuclei (arrowheads) and paraphyses with modified pit connections (arrows) in side view. 13-64: Enlarged pit connection (arrowhead) between gonimoblast filament and fusion cell.

(Maggs & Guiry 1985). Following fertilization (Fig. 13-71) the carpogonium and its first derivative fuse with nearby vegetative cells in the same branch system. The resulting fusion cell is multinucleate and issues uninucleate connecting filaments that are septate and branched (Fig. 13-72). Auxiliary cells are ordinary vegetative inner cortical cells. When a connecting filament approaches an auxiliary cell, the auxiliary cell forms a lateral process that fuses with the connecting filament. A cluster of go-

nimoblast filaments issues directly from the connecting filament near the point of fusion. In Fig. 13-73 two adjacent cortical cells function as auxiliary cells that have formed lateral processes. Only one has fused with the connecting filament.

The nemathecial families Rhizophyllidaceae (Wiseman 1977) and Peyssonneliaceae (Schneider & Reading 1987), Polyideaceae (Rao 1956) and the genus *Rhodopeltis* (Nozawa 1970) have separate carpogonial filaments and auxiliary cells interspersed

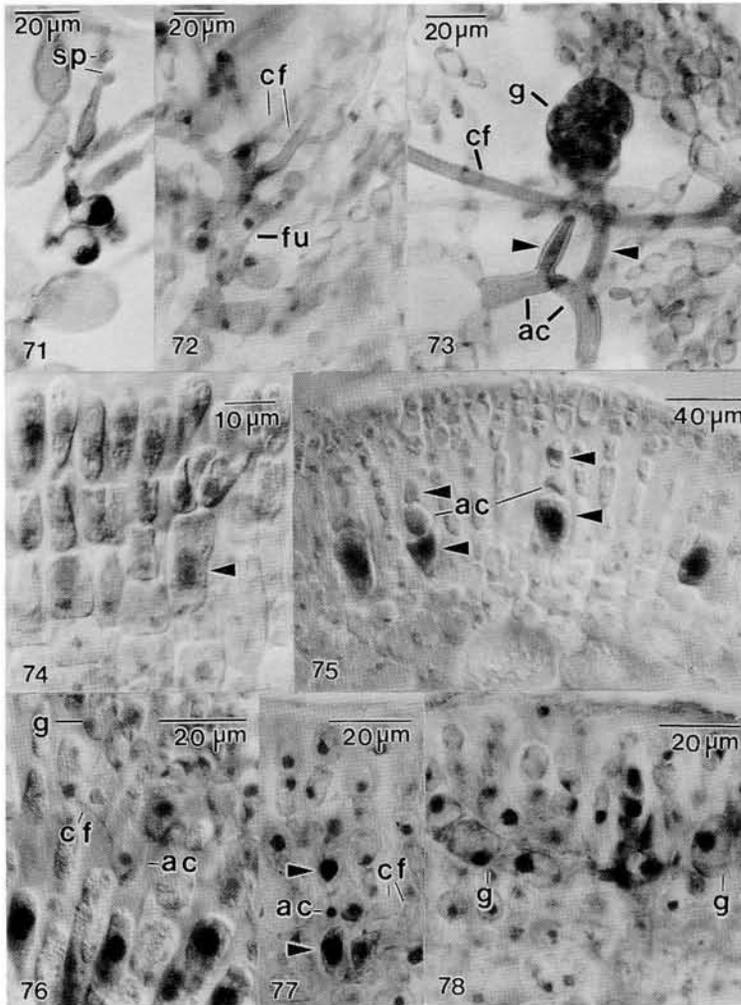


Figs. 13-65, 13-67. *Gelidium pteridifolium* (South Africa). 13-65: Carpogonium (cp), fused cortical cells (co), gonimoblasts (g) and nutritive filaments. 13-67: Fusion between terminal gonimoblast and terminal nutritive cells (arrow). Figs 13-66, 13-68 to 13-70. *Suhria vittata* (South Africa). 13-66: Carpogonium (cp), fused cortical cells (co), gonimoblasts (g), and nutritive filaments. 13-68, 13-69: Fusions between gonimoblast cells and nutritive cells (arrows). 13-70: Cross section of cystocarp.

among assimilatory filaments within a common nemathecial pustule. *Portieria* (formerly *Chondrococcus*; see Silva et al. 1987) is representative of the Rhizophyllidaceae. The nuclei are enlarged in the basal cell of the carpogonial branch before fertilization (Fig. 13-74), and the cells on either side of the auxiliary cell contain enlarged nuclei in *Portieria* (Figs. 13-75, 13-76) and in *Peyssonnelia* of the Peyssonneliaceae (Fig. 13-77). Gonimoblasts develop

directly from the connecting filaments in the vicinity of the auxiliary cells in both genera (Figs. 13-76, 13-78).

Acrosymphyton has recently been removed from the Dumontiaceae to the Acrosymphytaceae (Lindstrom 1986). Carpogonial branches and auxiliary cell branches are initially unbranched filaments that arise from inner cortical cells near the thallus apex (Fig. 13-79). Whereas auxiliary cell branches tend to



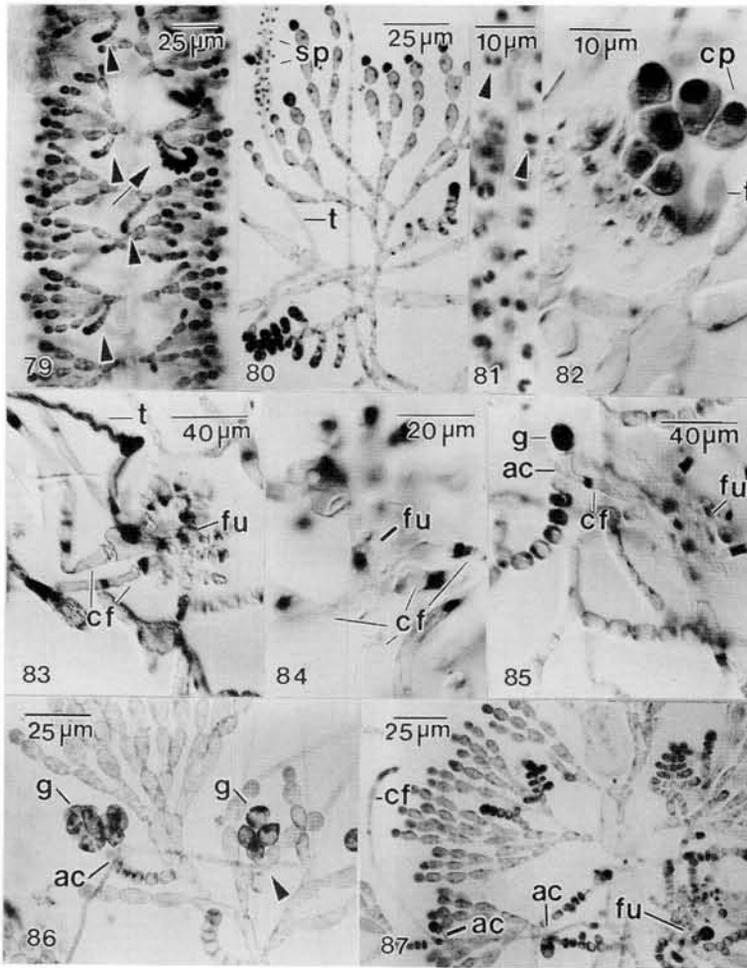
Figs. 13-71 to 13-73. *Schmitzia hiscockiana* (Bardsey, Wales, material provided by C. Maggs, photographs by M. Knauss). 13-71: Carpegonial branch and carpegonium with attached spermatia (*sp*). 13-72: Carpegonial fusion cell (*fu*) with connecting filaments (*cf*). 13-73: Auxiliary cells (*ac*) with processes (arrowheads) and connecting filament (*cf*) with gonimoblast (*g*).

Figs. 13-74 to 13-76. *Portieria (Chondrococcus) hornemannii* (South Africa). 13-74: Nemathecium with carpegonial branch. Note enlarged nucleus in basal cell (arrowhead). 13-75: Nemathecium with auxiliary cell branches and auxiliary cells (*ac*) with adjoining nutritive cells (arrowheads). 13-76: Connecting filament (*cf*), auxiliary cell (*ac*) and gonimoblasts (*g*).

Figs. 13-77, 13-78. *Peyssonnelia dubyi* (Northern Ireland, material provided by C. Maggs). 13-77: Connecting filament (*cf*) and auxiliary cell (*ac*) with adjoining nutritive cells (arrowheads). 13-78: Developing gonimoblasts (*g*).

remain unbranched, the carpegonial branches produce opposite laterals except for the carpegonium and its two subtending cells (Fig. 13-80). The trichogyne is long and spirally coiled, and numerous spermatia can attach to its sides (Fig. 13-80).

Individual spermatia are binucleate and appear to be in arrested telophase (Fig. 13-81). After fertilization the carpegonium and the more distal cells of the carpegonial branch are deeply staining and contain enlarged nuclei, whereas the proximal cells

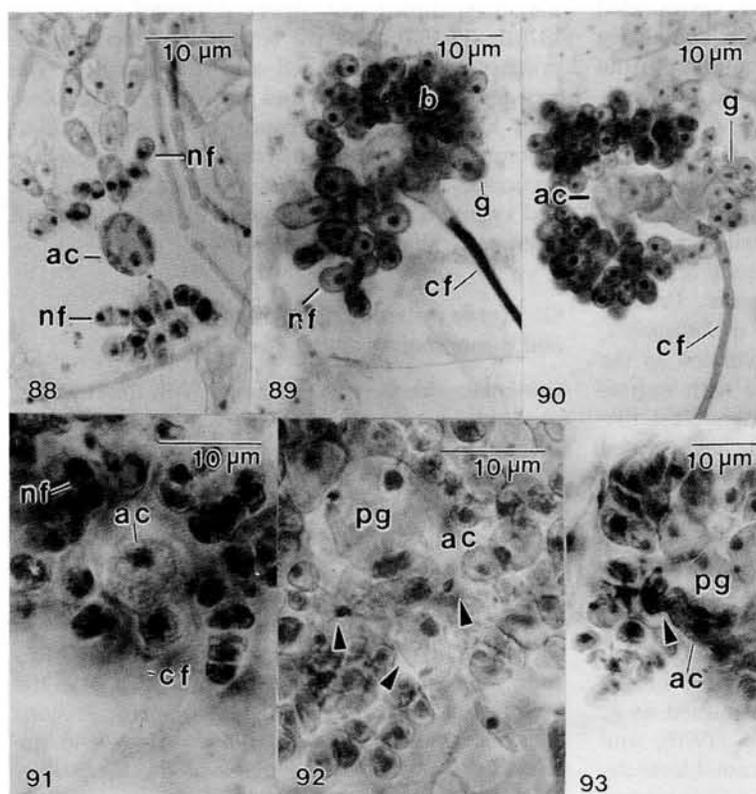


Figs. 13-79 to 13-87. *Acrosymphyton caribaeum* (Florida). 13-79: Young carpogonial branch (arrow) and auxiliary cell branches (arrowheads). 13-80: Spermatia (sp) attached to trichogyne (t). 13-81: Enlarged view of trichogyne in Fig. 13-80, showing binucleate spermatia (arrowheads). 13-82: Differentiated carpogonial branch and carpogonium (cp) with trichogyne (t). 13-83 to 13-85: Carpogonial fusion cell (fu) and connecting filaments (cf). 13-86, 13-87: Auxiliary cells (ac), connecting filaments (cf), and developing gonimoblasts (g). (Note gonimoblast remote from auxiliary cell in Fig. 13-86, arrowhead).

are vacuolate with small nuclei (Fig. 13-82). Processes emerging from the fertilized carpogonium fuse only with vacuolate cells, forming a fusion cell that, in turn, gives rise to numerous connecting filaments (Figs. 13-83 to 13-85). The auxiliary cell is a terminal cell of an auxiliary cell branch in which the subtending cells contain proteinaceous granules (Fig. 13-85). When a connecting filament passes close to an auxiliary cell, the auxiliary cell sends out a process that fuses with it. A gonimoblast initial is usually cut off in close proximity to

the auxiliary cell (Figs. 13-85, 13-86) but may be produced at a distance from it (Fig. 13-86). A connecting filament can branch independently of the auxiliary cell, unite with several auxiliary cells, and bear many gonimoblasts (Fig. 13-87).

The genus *Predaea* (Nemastomataceae) is unusual in having clusters of small-celled nutritive filaments produced on cortical cells above and below the auxiliary cell before fertilization (Fig. 13-88) that expand after contact by a connecting filament (Figs. 13-89, 13-90). Ultrastructural studies



Figs. 13-88 to 13-90. *Predaea feldmannii* (North Carolina, material provided by R. Searles), 13-88: Auxiliary cell (ac) and nutritive filaments (nf). 13-89, 13-90: Auxiliary cell (ac), nutritive filaments (nf) and connecting filament (cf) with gonimoblasts (g).

Figs. 13-91 to 13-93. *Grateloupia filicina* (South Africa). 13-91: Connecting filament (cf), auxiliary cell (ac), and ampullary nutritive filaments (nf). 13-92, 13-93: Fusions formed around pit connections (arrowheads) near auxiliary cell (ac) and primary gonimoblast cell (pg).

(Siotas & Wetherbee 1982) established that the pit connections between cells of the nutritive filaments break down and disappear at the time of gonimoblast formation, whereas the nuclei and cytoplasm remain intact. As in most species of *Predaea* (Kraft 1984), the connecting filament cuts off a single gonimoblast initial at its point of contact with the auxiliary cell in *P. feldmannii* (Fig. 13-89) and produces a compact cluster of gonimoblast filaments (Fig. 13-90).

Carpogonia and auxiliary cells are borne in separate clusters of filaments called ampullae in Halymeniaceae (Chiang 1970). After fertilization the carpogonium enlarges and fuses with its hypogynous cell in *Grateloupia*, and the resulting fusion cell emits numerous connecting filaments (Kraft 1977a). The auxiliary cell is a large subbasal

cell in an auxiliary cell ampulla that otherwise consists of small cells containing prominent nuclei (Fig. 13-91). A connecting filament cuts off a cell that fuses with the inner side of the auxiliary cell (Fig. 13-91). The gonimoblast initial is produced toward the outside and forms a compact cluster of gonimoblast filaments (Fig. 13-92). Channels develop progressively between the nutritive cells of the ampullary filaments commencing next to the auxiliary cell; however, unlike the development in *Predaea*, the fusions in *Grateloupia* take place alongside the primary pit connections (Figs. 13-92, 13-93).

Perhaps the most specialized system of preformed carpogonial and auxiliary cell branches is found in the Kallymeniaceae, a family that contains both procarpal and nonprocarpal genera (Norris 1957). In *Kallymenia reniformis* the auxiliary cell

apparatus consists of an auxiliary cell surrounded by a cluster of specially modified cells containing enlarged nuclei (Fig. 13-94). Correspondingly, the carpogonial branch system is composed of a supporting cell surrounded by a cluster of three-celled carpogonial branches in which the basal cell of each branch contains enlarged nuclei (Fig. 13-95). After fertilization, the basal cells of the carpogonial branches fuse with the supporting cell (Fig. 13-96) alongside the primary pit connections (Fig. 13-97) before producing connecting filaments. Primary connecting filaments are nonseptate in *Kallymenia*, with the nucleus and cytoplasm restricted to the filament tip (Fig. 13-98). They unite with remote auxiliary cells and produce the gonimoblast filaments. Womersley and Norris (1971) have illustrated the production of connecting filaments from the carpogonial fusion cell, their union with an auxiliary cell, and the direct development of gonimoblast filaments from the connecting filament in *Kallymenia cribrogloea*.

Gonimoblasts are produced directly from vegetative cells after the connecting filament has united with an auxiliary cell and contacted neighboring gametophytic cells in a *Kallymenia* identified as *K. reniformis* by Hommersand and Ott (1970), and auxiliary cells are absent and the gonimoblasts develop directly from vegetative cells in *Cirrulicarpus carolinensis* (Hansen 1977). In *Hommersandia maximicarpa* connecting filaments branch abundantly, become septate, and fuse with cells of special moniliform branches that, in turn, bear the gonimoblasts (Hansen & Lindstrom 1984). It appears that a nutritive system has evolved secondarily in these species, involving fusions with vegetative cells, either as a supplement to or as a replacement for the nutritive function of the auxiliary cell apparatus.

F. Transformed cortical cells: Plocamiaceae

A nutrient-processing center is generated soon after fertilization through the transformation of ordinary cortical cells adjoining the auxiliary cell in the Plocamiaceae, a procarpal family that is traditionally placed in the Gigartinales. The auxiliary cell is the supporting cell of a three-celled carpogonial branch in *Plocamium* (Kylin 1923). After diploidization, the auxiliary cell cuts off a uninucleate gonimoblast initial and itself becomes multinucleate (Fig. 13-99). At the same time the nucleus in each of the adjoining cortical cells enlarges (Figs. 13-99, 13-100). The cells with their modified nuclei persist throughout gonimoblast development (Fig. 13-101) and are prominent at the base of the go-

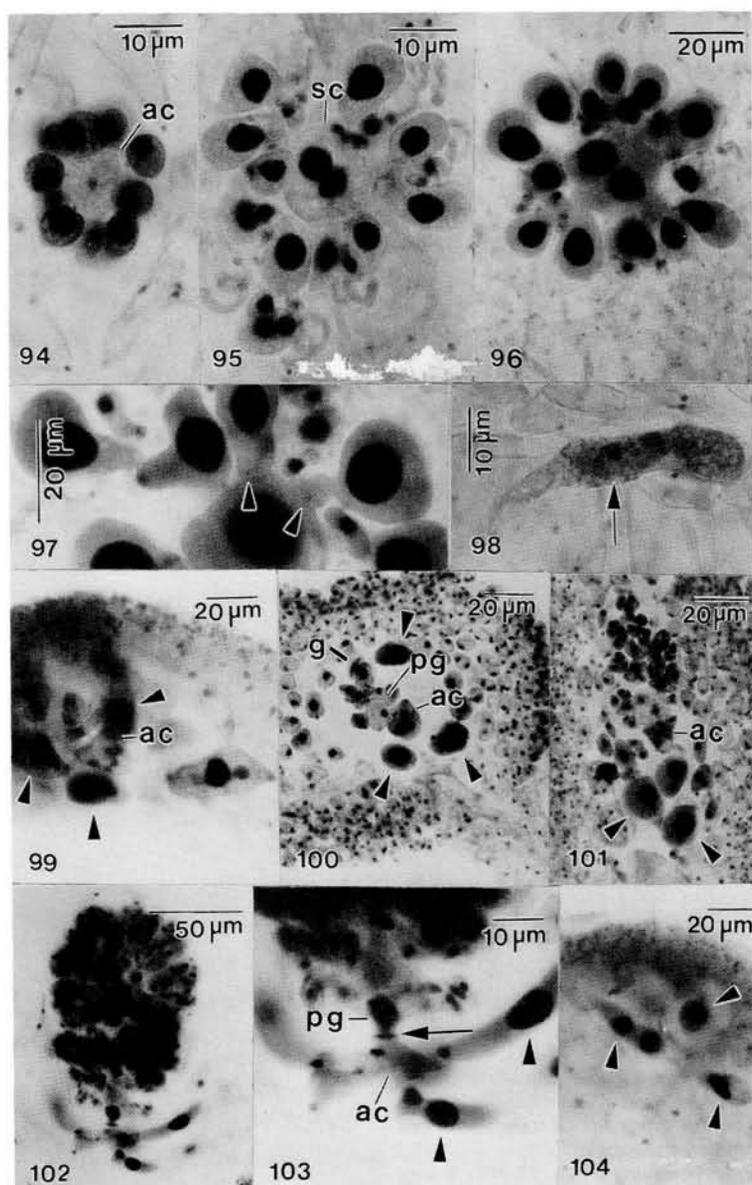
nomoblast during carpospore differentiation (Figs. 13-102, 13-103). The pit connection between the primary gonimoblast cell and the auxiliary cell broadens substantially, but no fusions take place (Fig. 13-103). Fertilized procarps commonly abort in branches in which an earlier fertilization has occurred. The formation of modified cortical cells and enlarged nuclei is triggered even in the event of an early abortion (Fig. 13-104).

G. Sterile nutritive filaments: Ceramiales and Bonnemaisoniales

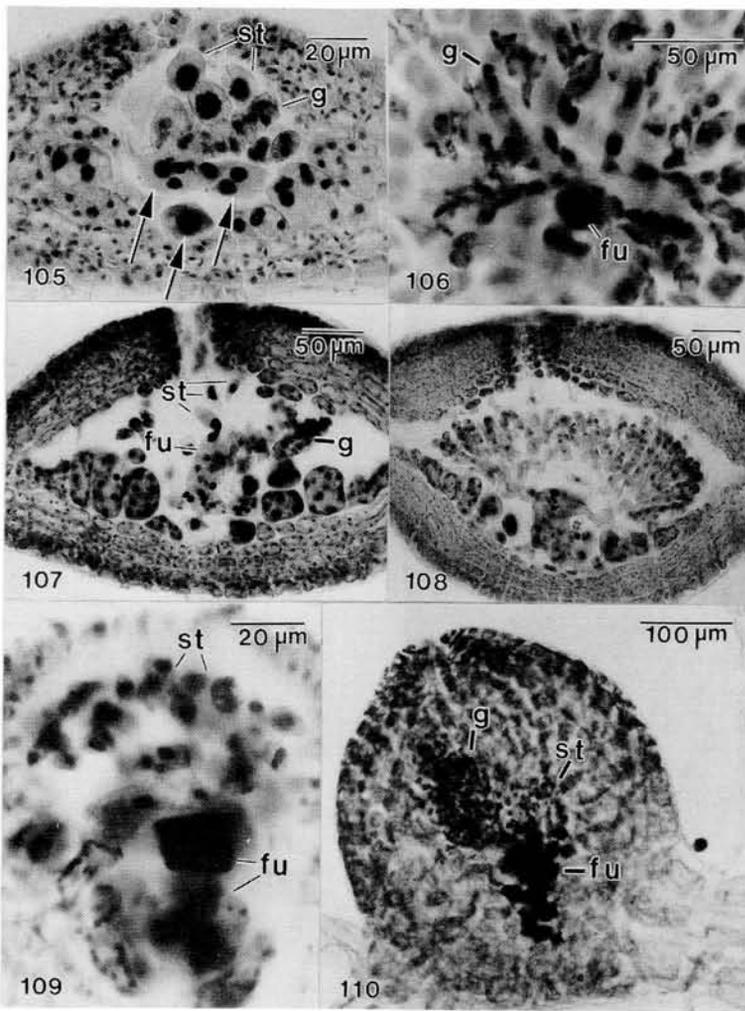
Cystocarp structure is correlated with thallus morphology in members of the Ceramiales. In the Delesseriaceae the thallus is a thin, membranous blade with ostiolate cystocarps protruding from one side or the other. The procarp consists of a supporting cell, lateral and basal sterile groups, and a four-celled carpogonial branch (Kylin 1956). In *Myriogramme* – and other genera of the Delesseriaceae that we have examined – the nucleus in each sterile group enlarges greatly after fertilization, followed by enlargement of the nuclei in the multinucleate central cells (Fig. 13-105). Fusions take place around the auxiliary cell as the gonimoblast ramifies in the plane of the blade (Fig. 13-106). Later, an ostiolate pericarp is formed from cortical cells and the central cells in the floor of the cystocarp, and their nuclei continue to enlarge (Fig. 13-107). Finally, many of these cells are incorporated into a prominent, multinucleate fusion cell as carposporangia form in chains (Fig. 13-108). The nutrient-processing function, which begins with the sterile cells, extends to the central cells in the floor of the cystocarp and finally to the large central fusion cell in successive stages of gonimoblast development.

Cystocarp formation was described earlier for the filamentous genus *Polysiphonia* (Section IX.C). Similarly, in *Heterosiphonia* (Dasyaceae) a pericarp composed of axial filaments is produced after fertilization. In contrast to *Polysiphonia*, the sterile groups of *Heterosiphonia* become extensively branched after fertilization, forming a tuft that fills the cavity of the young cystocarp (Fig. 13-109). The sterile filaments are still evident long after gonimoblasts have formed within the pericarp and fusions have taken place around the auxiliary cell (Fig. 13-110).

The Bonnemaisoniales have evolved a nutritive system similar to the one found in the Ceramiales. In *Naccaria* (Naccariaceae) the procarp consists of a supporting cell and a two-celled carpogonial



- Figs. 13-94 to 13-98. *Kallymenia reniformis* (Ireland). 13-94: Auxiliary cell apparatus and auxiliary cell (ac). 13-95: Supporting cell (sc) and carpogonial branches. 13-96: Carpogonial fusion cell. 13-97: Fusions around pit connections (arrowheads). 13-98: Tip of connecting filament containing nucleus (arrow).
- Figs. 13-99 to 13-101. *Plocamium cartilagineum* (Ireland). Auxiliary cell (ac), primary gonimoblast cells (pg), and developing gonimoblasts (g) surrounded by cortical cells with enlarged nuclei (arrowheads).
- Figs. 13-102 to 13-104. *Plocamium* sp. (New Caledonia). 13-102: Gonimoblasts removed from cystocarp. 13-103: Close-up of basal region in Fig. 13-102, showing auxiliary cell (ac), primary gonimoblast cell (pg) attached to auxiliary cell by a broad pit connection (arrow), and vegetative cells with enlarged nuclei (arrowheads). 13-104: Aborted fertilized procarp with modified cortical cells (arrowheads).

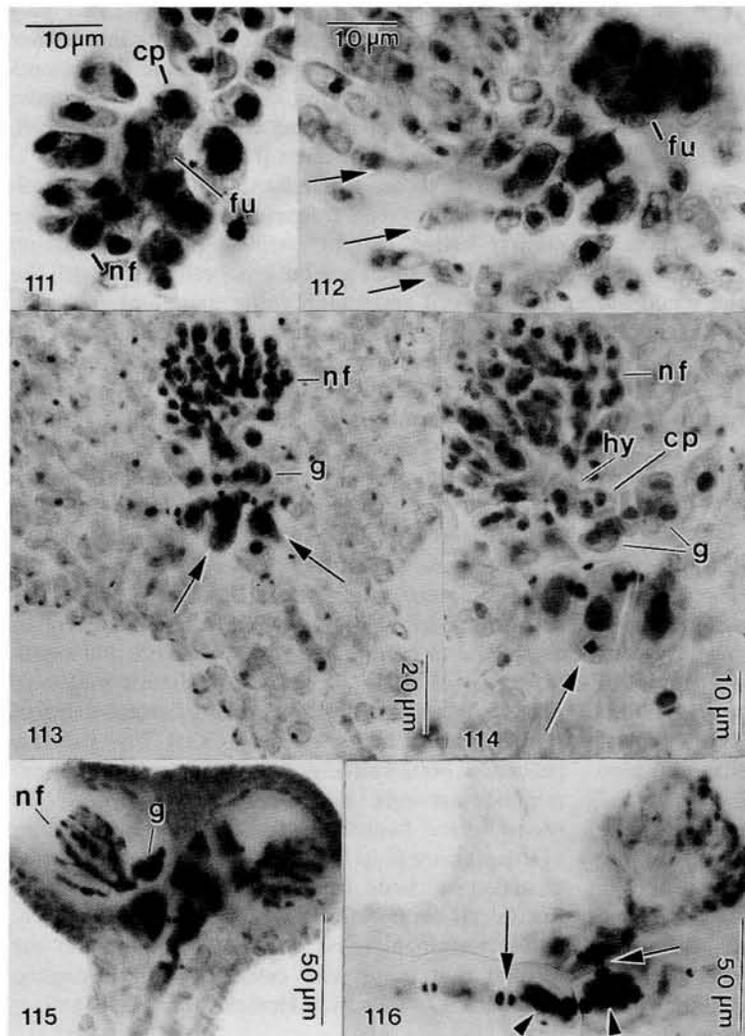


Figs. 13-105 to 13-108. *Myriogramme livida* (southern Chile). 13-105: Cross section of young cystocarp with gonimoblast (*g*). Note enlarged nuclei in sterile groups (*st*) and in floor of cystocarp (arrows). 13-106: Surface view of fusion cell (*fu*) bearing gonimoblasts (*g*). 13-107, 13-108: Cross section of cystocarp showing fusion cell (*fu*), developing gonimoblasts (*g*), and remnant sterile groups (*st*). Figs. 13-109, 13-110. *Heterosiphonia berkeleyi* (southern Chile). 13-109: Young cystocarp with fusion cell (*fu*) and sterile groups (*st*). 13-110: Older cystocarp with fusion cell (*fu*), sterile groups (*st*), and gonimoblasts (*g*) surrounded by pericarp.

branch. A small tuft of nutritive filaments is produced from the hypogynous cell before fertilization (Kylin 1928). After fertilization, the nuclei of all of the cells of the carpogonial branch apparatus enlarge, the carpogonium fuses with the hypogynous cell, and the nutritive cells are progressively incorporated into the fusion cell (Fig. 13-111). The supporting cell produces extensive secondary as-

simulatory filaments, and the nuclei in the basal cells of these filaments also enlarge (Fig. 13-112). Pit connections broaden between vegetative cells during gonimoblast development, followed by fusions that extend into the vegetative axis as the carposporangia mature.

Cystocarp development in *Bonnemaisonia asparagoides* (Bonnemaisoniaceae) is fundamentally the



Figs. 13-111, 13-112. *Naccaria wiggii* (Ireland, material provided by C. Maggs). 13-111: Carpogonium (*cp*) fused to carpogonial branch (*fu*) and nutritive filaments (*nf*). 13-112: Carpogonial fusion cell (*fu*) and secondary assimilatory filaments (arrows).

Figs. 13-113, 13-114. *Bonnemaisonia asparagoides* (Sweden). 13-113: Young cystocarps showing fusing nutritive filaments (*nf*), gonimoblast (*g*), and modified vegetative cells (arrows) within pericarp. 13-114: Later stage, after nutritive filaments (*nf*) have fused with hypogynous cell (*hy*) and carpogonium (*cp*).

Figs. 13-115, 13-116. *Bonnemaisonia nootkana* (California). 13-115: Young cystocarps with gonimoblast (*g*) and nutritive filaments (*nf*) seen in optical section. 13-116: Axial cells with modified pit connections (arrows) and enlarged nuclei (arrowheads).

same as in *Naccaria*. The hypogynous cell produces a tuft of nutritive filaments, and the cells below it initiate a pericarp before fertilization (Kylin 1916). At the same time that the carpogonium cuts off the

gonimoblast initial the nuclei in cells of the nutritive tuft enlarge, nearly filling each cell, and pit connections broaden between neighboring vegetative cells in the axis and basal cells of the developing

pericarp (Fig. 13-113). Pit connections between cells of the nutritive filaments break down, forming continuous channels at about the time that the carpogonium fuses with the hypogynous cell (Fig. 13-114). Also, the pit connections between the axial cells expand, becoming dome-shaped, and the nuclei enlarge (Fig. 13-114). Young gonimoblast and candelabra-like fused nutritive filaments surrounded by a pericarp are seen in optical section in *Bonnemaisonia hamifera* (Fig. 13-115). The nuclei and pit connections of the axial cells enlarge while the nuclei in the tuft of nutritive filaments degenerate (Fig. 13-116). Later, inner gonimoblast cells and axial cells will fuse to produce a large central fusion cell as the terminal carposporangia mature (Kyllin 1916).

H. Fusion cells: Gigartinales

Fusions between nutritive cells like the ones described earlier in *Predaea* or *Grateloupia* (Section X.E) leave the bounding outline of the filamentous system intact. More often, the initial fusion broadens or the fusions are extended to produce a fusion cell with a continuous outline. Progressive fusions involving the auxiliary cell, the inner gonimoblast cells, and adjoining gametophytic cells may give rise to a prominent central fusion cell.

In *Gloiosiphonia capillaris* (Gloiosiphoniaceae) the carpogonium and auxiliary cell are borne in the same filament cluster (Figs. 13-117, 13-119). The nucleus in the hypogynous cell is enlarged (Figs. 13-118, 13-119) and the carpogonium would normally support the production of connecting filaments (Edelstein 1972); however, the material from British Columbia illustrated here is apparently apomictic, like one of the strains described by DeCew et al. (1981), and lacks connecting filaments. Gonimoblasts are initiated before fusions commence (Fig. 13-120). The primary gonimoblast cell first fuses with the auxiliary cell, followed by progressive fusion between cells of the auxiliary cell branch and the inner gonimoblast cells (Figs. 13-121, 13-122). All fusions take place alongside the primary pit connections (Fig. 13-121). Later, fusions extend to include the inner gonimoblast cells (Fig. 13-123). Modified pit connections separate the outer gonimoblast cells, which mature into carposporangia, from the inner gonimoblast cells, which are incorporated into the fusion cell, leaving remnant pit plugs within the gonimoblast fusion cell (Delivopoulos & Kugrens 1985).

A much larger fusion cell is formed in *Gloiopeltis*

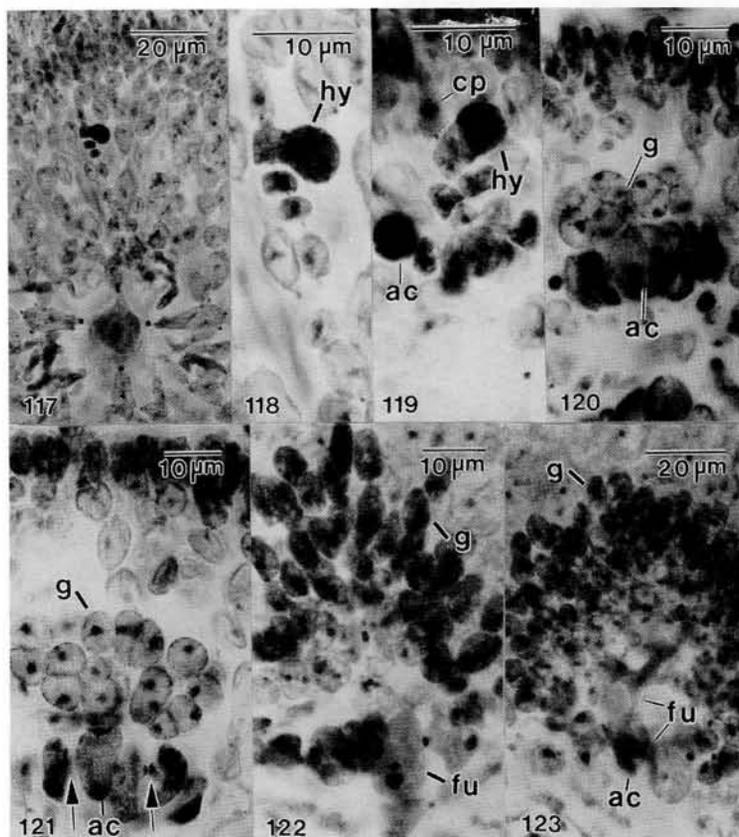
(Endocladiaceae), incorporating a substantial portion of the inner gonimoblast filaments in addition to cells of the auxiliary cell apparatus. Pit connections between adjoining cells do not degenerate; they remain well defined within the fusion cell, even in mature cystocarps (Figs. 13-124, 13-125).

Cystocarps are stalked and have thick multicellular pericarps with transverse ostioles and a large central fusion cell in *Heringia* (Caulacanthaceae) (Fig. 13-126). Inner gonimoblast cells unite with the auxiliary cell and neighboring gametophytic cells, forming a central fusion cell (Searles 1968); the outer gonimoblast filaments ramify among the surrounding vegetative filaments and produce carposporangia terminally in short chains (Figs. 13-127, 13-128). The cortical filaments and central fusion cell appear to function as a conduit between the photosynthetic pericarp and the outwardly radiating gonimoblast filaments.

Most genera of the Solieriaceae (including the Rhabdoniaceae) are characterized by a large central fusion cell (Min-Thein & Womersley 1976). In *Solieria* inner gonimoblast cells fuse with the auxiliary cell, which in turn fuses both inwardly and outwardly with cells of the bearing cortical filament (Gabrielson & Hommersand 1982a). The primary pit connections between the auxiliary cell, the inner gonimoblast cells, and the adjoining cortical cells broaden, and fusion takes place through the center of the pit plug (Fig. 13-129). Cells become confluent as fusion proceeds, leading to formation of a central fusion cell supported by a basal stalk (Fig. 13-130). Later, terminal sterile gonimoblast filaments are formed that unite with cells of the surrounding involucre (Gabrielson & Hommersand 1982a).

I. Special nutritive tissues: Ahnfeltiales and Gracilariales

Maggs and Pueschel (1989) demonstrated that the life history of *Ahnfeltia plicata* involves an alternation of generations between erect male (50%) and female (50%) gametophytes, a nemathecial carposporophyte and a crustose tetrasporophyte. Gonimoblast filaments develop directly from the carpogonium and grow over the outermost cortical cells, fusing with them and with each other to produce a complex fusion tissue. This tissue gives rise to outwardly growing filaments that terminate in diploid carposporangia (Maggs & Pueschel 1989). The fusion tissue corresponds to the "primary nemathecium," the outwardly growing filaments to the "secondary nemathecium," and the car-

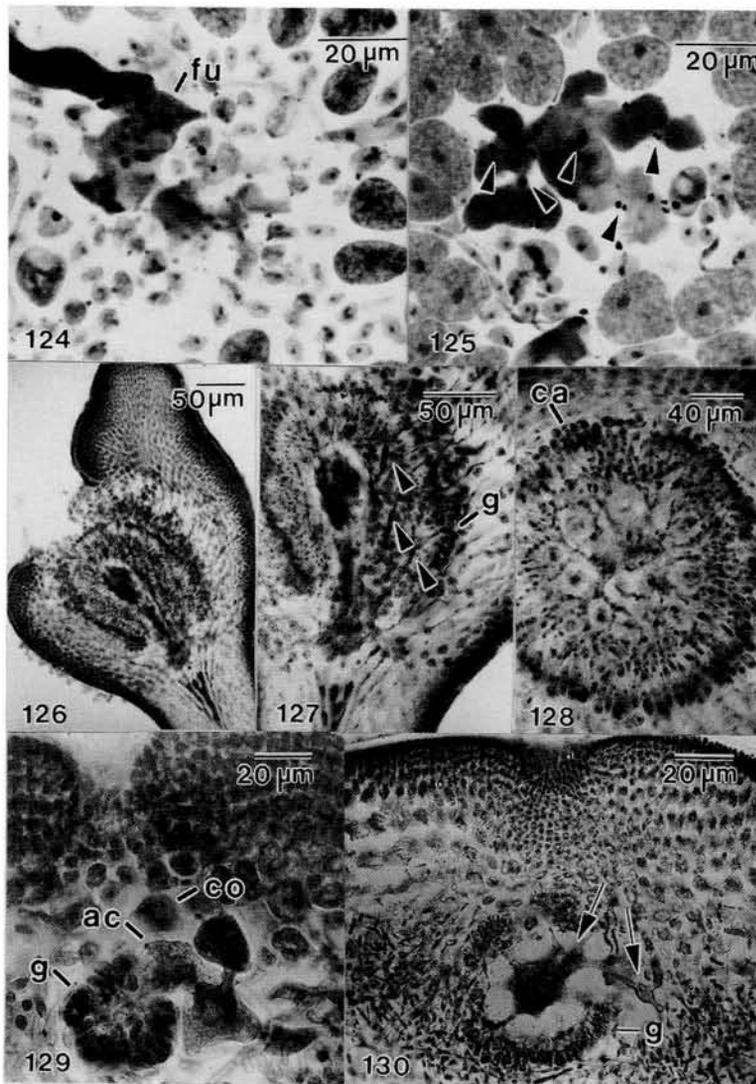


Figs. 13-117 to 13-123. *Gloiosiphonia capillaris* (British Columbia). 13-117, 13-118: Cross section of fertile area with enlarged hypogynous cell (*hy*). 13-119: Filament cluster containing carpoogonium (*cp*), hypogynous cell (*hy*) and auxiliary cell (*ac*). 13-120 to 13-123: Stages in fusion cell (*fu*) formation around the auxiliary cell (*ac*) and gonimoblast (*g*) development. (Note fusions around pit connections in Fig. 13-121, arrows.)

posporangia to the "monosporangia" of Rosenvinge (1931).

The Gracilariaceae, traditionally placed in the Gigartinales (Kylin 1956), is now placed in the Gracilariales (Fredericq & Hommersand 1989). In *Gracilaria verrucosa* the carpoogonial branch is a two-celled filament borne on a supporting cell that also bears a pair of sterile filaments surrounding the carpoogonium and typical auxiliary cells are absent (Fredericq & Hommersand 1989; Sjöstedt 1926). After fertilization, the carpoogonium enlarges and initially fuses with cells of the adjacent sterile filaments while the zygote nucleus is displayed prominently in the center of the fusion cell (Fig. 13-131). Additional fusions with neighboring gametophytic cells lead to the formation of a large, lobed

fusion cell containing both diploid and haploid nuclei in *G. verrucosa* (Fig. 13-132). Such fusions take place around existing pit connections, which may persist and are readily seen inside the fusion cell (Fig. 13-133). Several uninucleate gonimoblast initials are cut off from lobes of the multinucleate fusion cell (Fig. 13-134), and these produce compact gonimoblasts initially composed of uninucleate cells (Fig. 13-135). A prominent pericarp is formed to the outside by transverse division of the apical cells of cortical files (Figs. 13-131, 13-132, 13-135). After the gonimoblasts have expanded, filling the cystocarp cavity, they initiate chains of carposporangia and also produce tubular nutritive cells that fuse with pericarp cells (Fig. 13-136) or with cells in the floor of the cystocarp (Fig. 13-137).



Figs. 13-124, 13-125. *Gloiopeltis furcata* (California). Fusion cell (*fu*) formed around persistent pit connections (arrowheads).

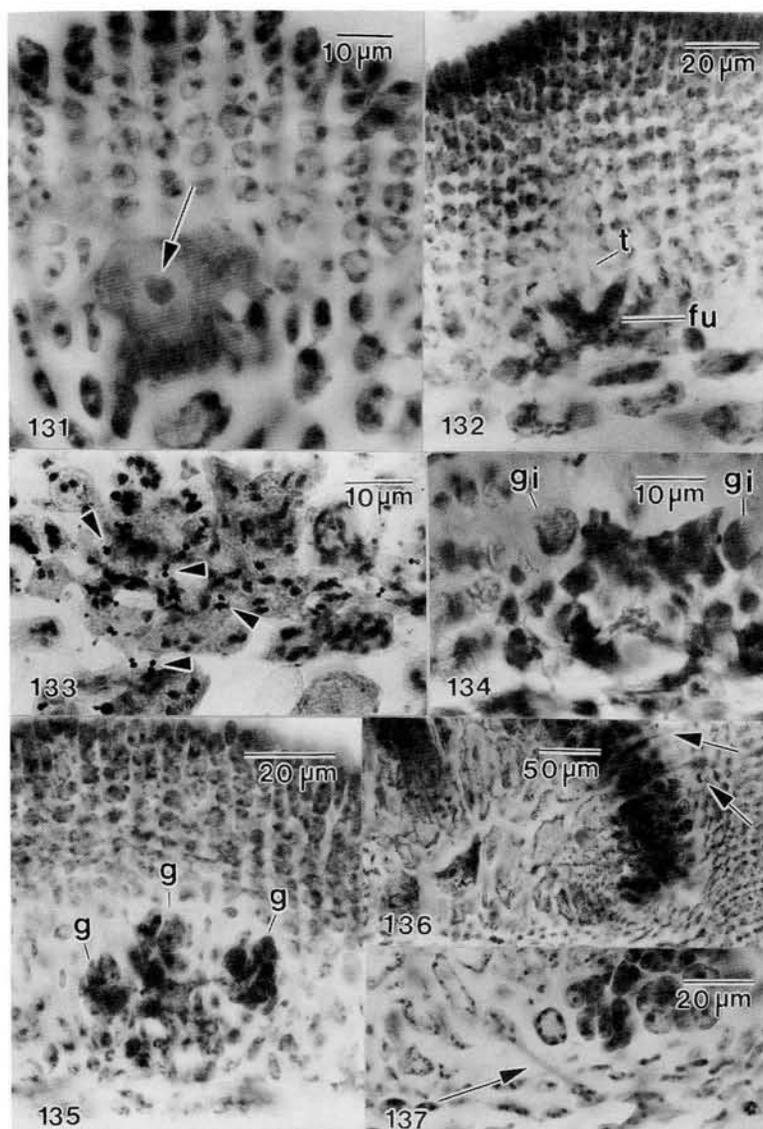
Figs. 13-126 to 13-128. *Heringia mirabilis* (South Africa). 13-126, 13-127: Longitudinal section of cystocarp with gonimoblasts (*g*), central fusion cell, and elongated cortical filaments (arrowheads). 13-128: Cross section of cystocarp showing ramifying gonimoblasts bearing carposporangia (*ca*).

Figs. 13-129, 13-130. *Solieria australis* (Natal, South Africa, material provided by G. Lambert). 13-129: Early stage showing fusions through pit connections between auxiliary cell (*ac*), young gonimoblast (*g*), and vegetative cortical cells (*co*). 13-130: Older fusion cell (arrows) and gonimoblasts (*g*).

J. Nutritive tissues and fusion cells: Rhodymeniales

The auxiliary cell in Rhodymeniales is the terminal cell of a two-celled filament borne on the supporting cell of a three- to four-celled carposogonial branch

(Kylin 1956). A supporting cell bearing a three-celled carposogonial branch is illustrated in *Rhodymenia* (Fig. 13-138). Transfer of the diploid nucleus from the fertilized carposogonium to the auxiliary cell is mediated by a connecting cell (Sparling 1957). The supporting cell, auxiliary mother cell, and



Figs. 13-131 to 13-137. *Gracilaria verrucosa* (Ireland and Wales, material provided by J. Brodie and E. Jones). 13-131: Fertilized carpogonium containing zygote nucleus (arrow). 13-132: Young fusion cell (*fu*) and trichogyne remnant (*t*). 13-133: Fusion cell formed around pit connections (arrowheads). 13-134, 13-135: Gonimoblast initials (*gi*) and young gonimoblasts (*g*). 13-136, 13-137: Gonimoblasts with tubular nutritive cells (arrows).

auxiliary cell enlarge, a protein body forms in the auxiliary cell, and a primary gonimoblast cell is cut off that retains the protein body (Fig. 13-139). At the same time an external pericarp is produced and a nutritive tissue forms in the floor of the cystocarp, composed of deeply staining, multinucleate vegeta-

tive cells (Fig. 13-139). As the gonimoblasts develop, the auxiliary cell, auxiliary mother cell, and supporting cell fuse, and the nutritive cells commence to fuse with one another and with the supporting cell (Figs. 13-140, 13-141). The protein body persists inside the primary gonimoblast cell, and the

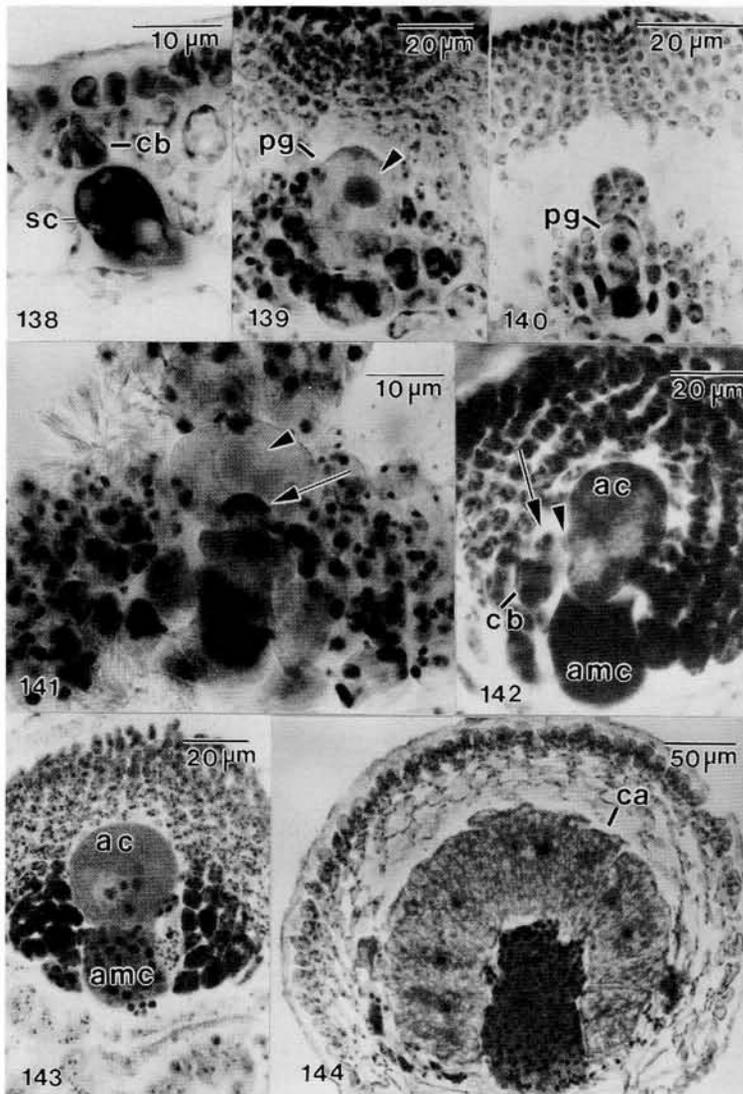
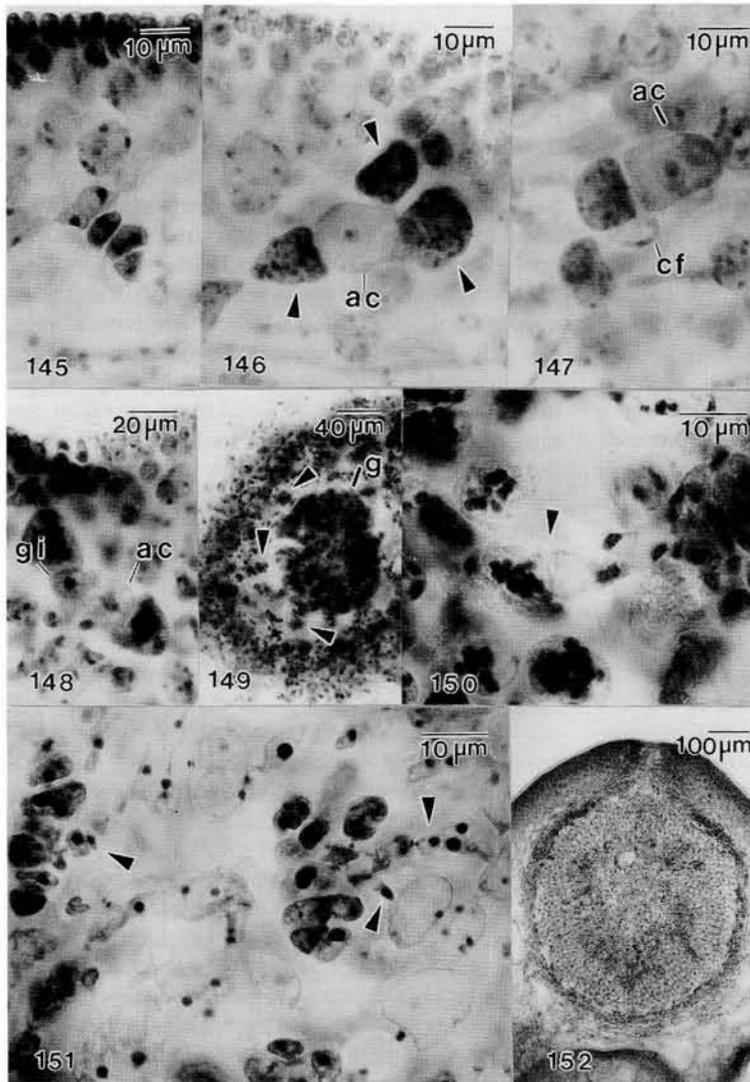


Fig. 13-138. *Rhodymenia pseudopalmeta* ssp. *caroliniana* (North Carolina); supporting cell (sc), carpogonial branch (cb).

Figs. 13-139 to 13-141. *Rhodymenia howeana* (Chile), 13-139: Cross section of young cystocarp showing primary gonimoblast cell (pg) with protein body (arrowhead) surrounded by nutritive tissue. 13-140: Primary gonimoblast cell (pg) bearing gonimoblasts. 13-141: Close-up of multinucleate nutritive cells and primary gonimoblast cell with protein body (arrowhead) and modified pit connection (arrow).

Figs. 13-142 to 13-144. *Chylocladia verticillata* (Ireland). 13-142: Fused carpogonial branch with connecting cell (arrow), auxiliary mother cell (amc), and auxiliary cell (ac) with process (arrowhead). 13-143: Young cystocarp showing auxiliary mother cell (amc) and auxiliary cell (ac) surrounded by nutritive tissue. 13-144: Mature cystocarp with fusion cell and carposporangia (ca).



Figs. 13-145 to 13-152. *Agardhiella subulata* (North Carolina, collected by P. Gabrielson). 13-145: Carpogonial branch. 13-146: Auxiliary cell (ac) and adjacent multinucleate cells (arrowheads). 13-147: Connecting filament (cf) approaching auxiliary cell (ac). 13-148: Auxiliary cell (ac) and gonimoblast initial (g). 13-149: Gonimoblasts (g) and secondary nutritive filaments (arrowheads). 13-150: Gonimoblast cell fusing with vegetative nutritive cell (arrowhead). 13-151: Later stage, gonimoblast filaments cutting off conjuctor cells that fuse with vegetative cells (arrowheads). 13-152: Cross section of mature cystocarp.

pit plug between it and the auxiliary cell broadens dramatically (Fig. 13-141). In *Rhodymenia* the fused nutritive cells with their enlarged nuclei persist up to the final stages of carposporangial maturation and evidently function as a major nutrient-processing center.

We have seen a stage in *Chylocladia* (Champiaceae) with an expanded auxiliary cell and fused carpogonial branch with a connecting cell (Fig. 13-142). A process extends from the auxiliary cell toward the connecting cell, perhaps to initiate fusion. The auxiliary mother cell and the surrounding

nutritive cells become multinucleate and deeply staining prior to gonimoblast formation (Figs. 13-142, 13-143) and appear to function as a primary nutrient-processing center. Unlike the case in *Rhodymenia*, the cystocarp subsequently forms a large, multinucleate central fusion cell bearing sessile carposporangia at maturity (Fig. 13-144). This fusion cell becomes deeply staining and filled with nuclei as the contents of the surrounding nutritive cells are depleted. It appears to function as a secondary nutrient-processing center.

K. Placentae: Gigartinales

In several families belonging to the order Gigartinales individual gonimoblast cells either fuse directly with noncontiguous gametophytic cells or become linked to them by means of secondary pit connections to form a network in the center or at the base of the cystocarp. Kraft (1977b) referred to such a structure, composed of intermixed, fused carposporophyte and gametophyte tissues having a nutritive function, as a placenta.

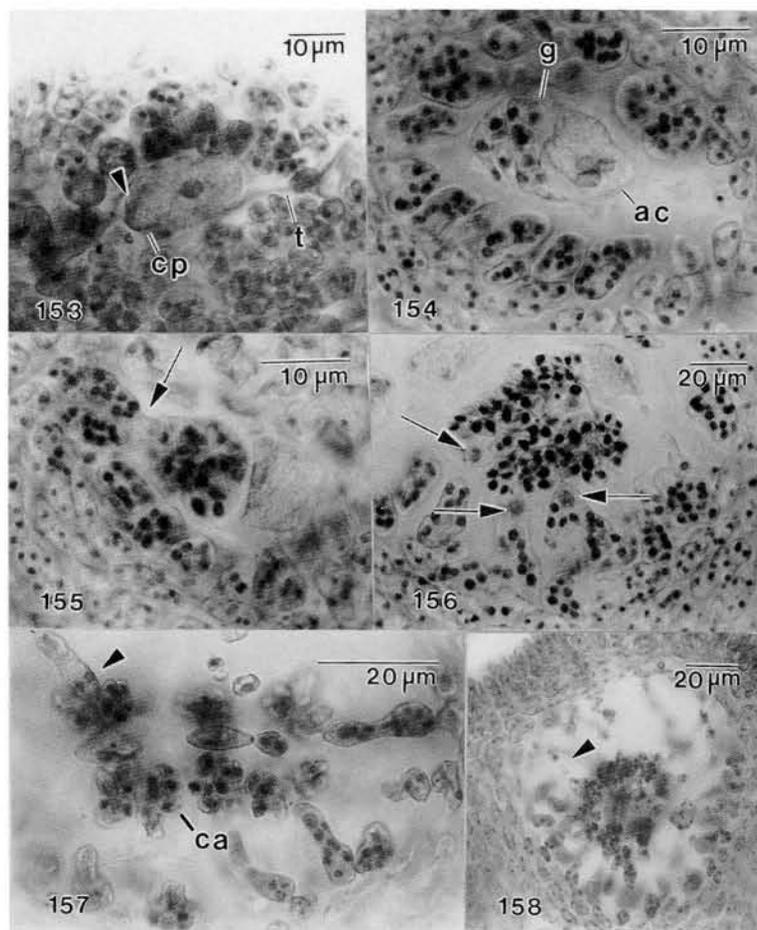
A good example of placental development is provided by the genus *Agardhiella*, one of the few genera of the Solieriaceae to have a central placenta instead of a fusion cell. The carpogonial branch is directed inward and is typically three-celled with a reflexed trichogyne (Fig. 13-145), and auxiliary cells are borne in separate primary cortical filaments (Fig. 13-146). Cells proximal and distal to the auxiliary cell become filled with nuclei as a result of synchronous nuclear divisions and are deeply staining prior to diploidization (Fig. 13-146). In *Agardhiella* the fertilized carpogonium produces two connecting filaments that are unbranched and nonseptate (Gabrielson & Hommersand 1982b). A connecting filament contacts an auxiliary cell at its proximal end (Fig. 13-147), and a gonimoblast initial is cut off from the distal end (Fig. 13-148). Inner cortical cells generate files of secondary filaments that grow toward the developing gonimoblast (Fig. 13-149). Terminal, uninucleate gonimoblast cells contact and fuse with the files of multinucleate gametophytic cells (Figs. 13-149, 13-150). Later, as the cystocarp expands, small conjuctor cells are cut off from gonimoblast filaments that fuse with neighboring vegetative cells that are now enlarged and vacuolate (Fig. 13-151). The mature cystocarp is ostiolate and has a cellular center composed of a placenta of gonimoblast and vegetative cells bearing carposporangia in short chains surrounded by a stretched outer involucre (Fig. 13-152). Sterile gonimoblast filaments extend and fuse with the involu-

cral cells during the final stages of carposporangial maturation (Gabrielson & Hommersand 1982b). The nutritive system described above consists of four compartments, each of which is produced and functions at a particular stage of carposporophyte development.

The families Cystocloniaceae and Hypneaceae have procarps in which the auxiliary cell is situated distal to the supporting cell of a three-celled carpogonial branch (Kylin 1956). In *Hypnea* the fertilized carpogonium fuses directly with the auxiliary cell at its proximal end (Fig. 13-153). Inner cortical cells generate a special nutritive tissue composed of multinucleate cells beneath the developing gonimoblast (Fig. 13-154). Uninucleate, terminal gonimoblast cells fuse with the multinucleate cells of the nutritive tissue (Figs. 13-155, 13-156). Later, as the cystocarp expands, clusters of gonimoblast filaments differentiate into carposporangia, and a few form sterile nutritive filaments that will fuse with cells of the pericarp (Figs. 13-157, 13-158).

The Australasian families Acrotylaceae (Kraft 1977b), Dicranemaceae (Kraft 1977c), and Mychodeaceae (Kraft 1978) have placental cystocarps in which fusions between gonimoblast filaments and vegetative cells are abundant. In the polycarpogonial genus *Mychodea* (Mychodeaceae) the supporting cell is an enlarged, multinucleate inner cortical cell that bears a cluster of three-celled carpogonial branches (Figs. 13-159, 13-160). The supporting cell functions as the auxiliary cell (Kraft 1978), which generates gonimoblast filaments that ramify inwardly among the surrounding gametophyte tissues (Figs. 13-161, 13-162) and unite with vegetative cells by means of secondary pit connections (Fig. 13-163). Gonimoblast cells are initially uninucleate, whereas the vegetative cells are all multinucleate (Figs. 13-162, 13-163). Carposporangia are produced in clusters associated with the gametophytic cells (Kraft 1978). Some of the gonimoblast filaments elongate and unite with vegetative cells toward the periphery of the cystocarp at the stage of carpospore differentiation (Fig. 13-164).

Some members of the Phyllophoraceae produce ordinary cystocarps, whereas others produce an external pustule bearing tetrasporangia (Ardré 1978). *Gymnogongrus patens* is representative of members of the Phyllophoraceae in which the gonimoblast develops inwardly and produces masses of carposporangia (Fig. 13-165). As in *Mychodea*, the gonimoblast cells are initially uninucleate and the gametophytic cells are multinucleate (Fig. 13-166). Many gonimoblast cells fuse onto each vegetative cell, forming small fusion cells within the cystocarp



Figs. 13-153 to 13-158. *Hypnea musciformis* (North Carolina). 13-153: Carposogonium (cp) with trichogyne (t) fused to auxiliary cell (arrowhead). 13-154: Auxiliary cell (ac) and gonimoblast (g) surrounded by nutritive tissue. 13-155, 13-156: Fusions between nutritive cells and gonimoblast cells (arrows). 13-157, 13-158: Clusters of carposporangia (ca) and sterile gonimoblast filaments (arrowheads).

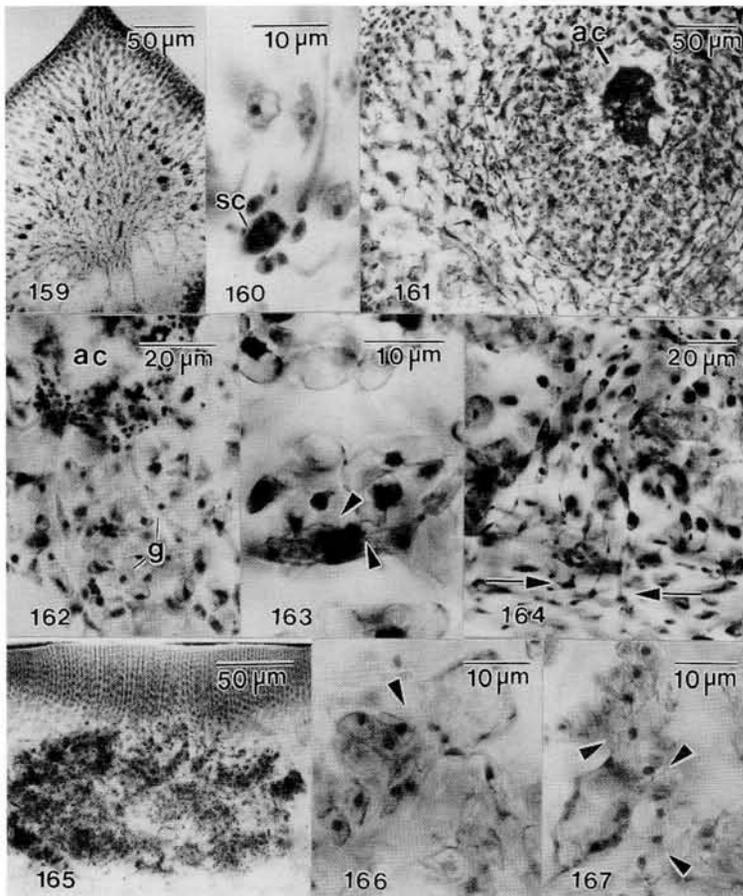
(Fig. 13-167) that serve as initiation sites for the production of carpospore-bearing filaments.

In species of *Chondrus* (Gigartinaeae) very fine gonimoblast filaments ramify through the medullary tissue, making secondary pit connections with medullary cells (Mikami 1965). The cystocarp is more compact in *Gigartina*. In *G. teedii* an extensive secondary tissue derived from subcortical and medullary cells forms around the diploidized auxiliary cell (Tsekos & Schnepf 1983). This tissue consists of clusters of deeply staining, multinucleate cells (Figs. 13-168, 13-169). Gonimoblast filaments composed of uninucleate cells develop directly from the auxiliary cell and grow in a compact formation between the clusters of vegetative cells (Figs. 13-168, 13-169). Later, the gonimoblast filaments cut off small conjuctor cells that fuse with enlarged, vacuolate vegetative cells, forming secondary pit connections at the same time that other

files of gonimoblast cells are being converted into carposporangia (Figs. 13-170, 13-171). The mature cystocarp is surrounded by a prominent involucre (Fig. 13-170). Secondary tissue formed around the fertilized procarp functions as the initial nutrient-processing center in *G. teedii*, with the auxiliary cell acting as a conduit to the young gonimoblast filaments. Later, secondary pit connections provide direct linkage between gonimoblast and gametophyte tissues. Finally, contact is made with cells of the involucre during the final stages of carpospore maturation.

XI. SUMMARY

Evolution of the sexual system in Rhodophyta has proceeded subject to two constraints. First, construction of the vegetative thallus is fundamentally filamentous, with growth initiated by apical cells in



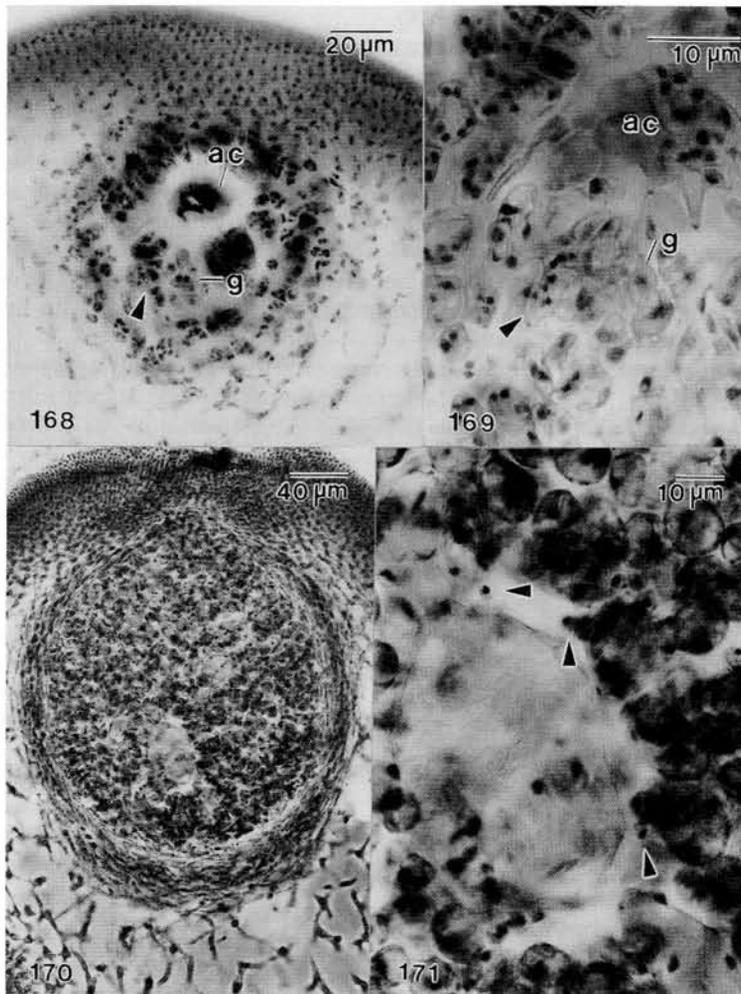
Figs. 13-159 to 13-164. *Mychodea carnosa* (South Australia). 13-159: Fertile female tip. 13-160: Supporting cell (sc) bearing carpogonial branches. 13-161, 13-162: Multinucleate auxiliary cell (ac) and uninucleate gonimoblast filaments (g) ramifying through medullary tissue. 13-163: Gonimoblast cells fused to vegetative cells (arrowheads). 13-164: Sterile gonimoblast cells fused to involucre cells (arrows).
Figs. 13-165 to 13-167. *Gymnogongrus patens* (Morocco). 13-165: Cross section of cystocarp. 13-166, 13-167: Uninucleate gonimoblast cells fused with multinucleate vegetative cells (arrowheads).

the principal subclass, Florideophycidae (Chapter 12). Second, fertilization is inherently inefficient in the absence of gamete motility, a limitation that has been partly compensated for by enhanced spore production associated with biphasic and triphasic life cycles (Searles 1980; Section I; see Chapter 17).

The principal reproductive features that unite the Rhodophyta are homologies in the ultrastructure and developmental pathways of spermatia, carpogonia, and spores of all types. In contrast, the differences in the position of reproductive cells on the thallus separate three major phylogenetic lines: (1) intercalary, with spores and male gametes

cut out one at a time by a curved wall (Rhodochaetales, Compsopogonales); (2) intercalary, in packets produced by successive perpendicular divisions (Bangiales); (3) terminal, transformed from apical initials (Florideophycidae). The localization of reproductive functions in apical initials in Florideophycidae is the key event in the evolution of this group that probably stabilized filamentous growth and led to carposporophyte formation and the triphasic life cycle (Section II).

We have argued that the primitive carposporophyte in Florideophycidae was an autotrophic, somatic phase corresponding to an asexual, branched



Figs. 13-168 to 13-171. *Gigartina teedii* (Morocco). 13-168, 13-169: Auxiliary cell (ac), uninucleate gonimoblasts (g), and multinucleate secondary vegetative cells (arrowheads). 13-170: Cross section of cystocarp. 13-171: Conjuncture cells (arrowheads) cut off from gonimoblast cells fusing onto large gametophytic cell.

filament bearing monosporangia (Section III). Its subsequent evolution involved increased nutritional dependency on the gametophyte. Some evolutionary lines retained the primitive condition in which gonimoblasts develop directly on the fertilized carpogonium; others evolved auxiliary cells and connecting cells or connecting filaments as a means of amplifying the products of a single fertilization (Section IV). Further evolution has involved the progressive modification of gametophytic tissues and the structural and functional compartmentalization of the cystocarp. We recognize three compartments: (1) the outer photosynthetic tissues, (2) modified inner gametophytic tissues that process and store the metabolites of photosynthesis, and (3) the developing carposporophyte (Section V).

In the first compartment light energy is used to absorb mineral nutrients from the environment and fix carbon dioxide, water, and mineral salts into organic molecules. Although it is possible that complex substances are transported to the carposporophyte through pit connections that link the tissues, we favor a model in which simple molecules are excreted from their "source" in the photosynthetic layers and diffuse along gradients to "sinks" composed of gametophytic tissues in the interior of the cystocarp. In reproductive thalli the sinks consist of specially modified cells or tissues that lie in close proximity to carpogonia or auxiliary cells or are so situated that they are readily contacted by developing gonimoblasts. The efficiency of the proposed model depends on the creation

of sinks that are strategically located to support carposporophyte development in competition with sinks that sustain vegetative growth or with the growing vegetative tip itself.

We have observed that carposporophyte growth is not a continuous process in most families of Florideophycidae. Rather, it proceeds in stages, with periods of rapid growth followed by intervals of slow growth or apparent inactivity during which the pattern of development may change. Each stage is preceded by the transformation of existing gametophytic cells into special protein-rich tissues, or new secondary gametophytic tissues are formed that are rich in protein content and often contain modified nuclei (Sections IX, X).

Nutritional tissues fall into two categories: those that are consumed in a single stage of carposporophyte development and those that persist and appear to function through several stages. Both usually contain cells that are rich in proteins, but the latter invariably have one or more enlarged nuclei containing amplified levels of DNA. We have called such a tissue a nutrient-processing center (Section V). The transformed tissues may be ordinary carpogonial branches; secondarily produced carpogonial or auxiliary cell branches; nematocial filaments; modified uninucleate vegetative cells, sterile "groups," or nutritive "tufts"; special multinucleate vegetative

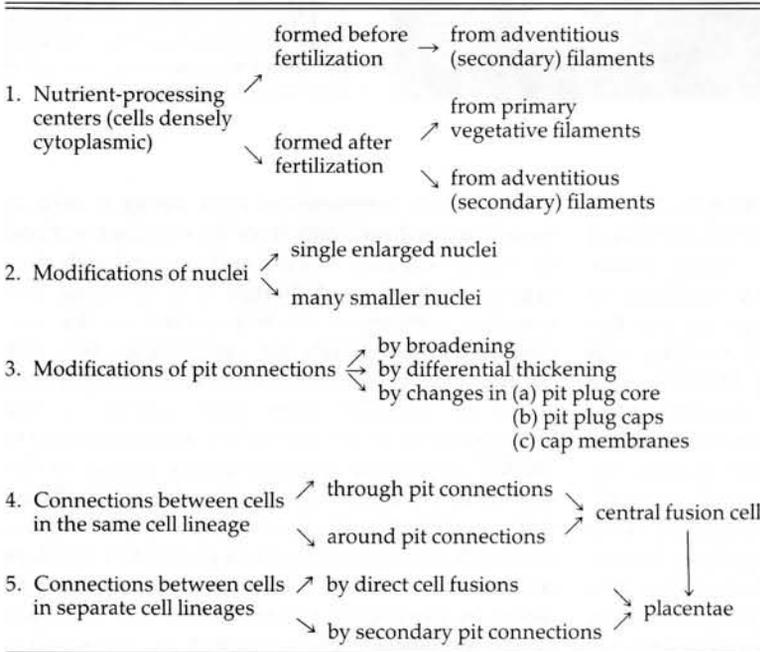
cells, filaments or tissues, and fusion cells or placentae (Section X).

Morphological evidence indicates that the transport of nutriment from nutritive tissues to the carposporophyte may involve (1) the enlargement and structural modification of existing pit connections, (2) fusions between contiguous cells either through or around primary pit connections, sometimes with formation of a central fusion cell, or (3) direct fusions or the formation of secondary pit connections between gonimoblast cells and non-contiguous gametophytic cells, sometimes with the formation of a well-defined placenta.

Fusion cells commonly undergo autolysis of their nuclei and other cell organelles, becoming vacuolate at a late stage of gonimoblast ontogeny, as in *Poly-siphonia* (Wetherbee 1980) or *Gloiosiphonia* (Delivopoulos & Kugrens 1985). Delivopoulos & Kugrens (1985) have expressed the opinion that a nutritive function cannot be ascribed to such fusion cells. We take an opposite view and interpret the ultrastructural evidence as indicating that fusion cell formation and organelle autolysis is a process of senescence designed to cannibalize compounds, particularly nitrogen-containing substances, for use during the final stages of carposporophyte development.

In some families of the Gigartinales, such as the

Table 13-1. Evolutionary trends in the nutrition of the carposporophyte



Solieriaceae, fusion cells have been replaced by placentae in the cystocarps of more advanced genera (Section X.K). Individual cystocarps are invariably larger and produce greater numbers of carpospores in families or genera with fusion cells or placentae than in related taxa that lack them.

Similar structures and nutritional strategies have evolved at different times in different groups of red algae. Indeed, convergent evolutionary themes appear to be the norm rather than the exception. Table 13-1 presents some alternative ontogenetic pathways that have produced morphologically similar cystocarps. It is clear in retrospect that Kylin possessed a highly developed nutritional concept of cystocarp morphology, which he used primarily in characterizing families. Many of the developmental characters that we have identified based on a functional model of cystocarp morphology apply to families and infrafamilial taxa recognized by Kylin (1956). A few call for taxonomic revisions.

XII. ACKNOWLEDGMENTS

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