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The Structure of *Alatocladia modesta*, an Articulated Coralline (Rhodophyta) Endemic to Japan

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Abstract

The monotypic *Alatocladia* (Corallinaceae, Rhodophyta) resembles *Calliarthron* in many aspects of morphology and anatomy. The intergenicula are relatively robust and usually flat and lobed. They have the usual features characteristic of the Corallinoideae, tribe Corallineae, except that the medullary filaments are twisted, as are also those in *Calliarthron*. Conceptacles are solely medullary, being both axial and marginal in origin. Development of conceptacles in tetrasporangial plants results in pores that are subapical and located on the faces of the intergenicula; this excentricity is sometimes present in sexual conceptacles also, but to a lesser extent. Gonimoblast filaments arise from the surfaces and margins of fusion cells. *Alatocladia* is probably most closely related to *Calliarthron*, with the presence of cortical as well as marginal conceptacles in the latter setting the two genera apart.

Introduction

The thalli of articulated coralline algae such as *Alatocladia* consist of coherent filaments growing into crustose holdfasts and segmented fronds made up of calcified intergenicula and uncalcified genicula. In a precise manner four types of vegetative cells are produced in terminal meristems at branch apices and intercalary meristems just below the lateral branch surfaces: medullary, cortical, epithallial, and genicular cells[1]. Reproductive cells form in conceptacles and also exhibit a great deal of precision in the way they develop. Conceptacles originate in various positions on the intergenicula, and the location of conceptacle primordia has been useful in delimiting the genera of articulated coralline algae[2]. In this paper we present the results of our structural study on the only species in *Alatocladia*, *A. modesta* (Yendo) Johansen[2], a genus known to have conceptacle primordia developing from medullary tissues in axial and marginal positions.

Among the 12 genera in the Corallinoideae (a subfamily in the Corallinaceae) *Alatocladia* is the least known structurally. *Alatocladia modesta* was described when Yendo[3] for the first time published on articulated coralline algae from Japan. Based on specimens from Hakodate and Kaifu he described *Cheilosporum anceps*

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var. *modestum* Yendo, considering it as new because of flat, sagittate intergenicula. Since then this taxon has received scant attention, being placed in *Calliarthron* by Manza[4] and in *Alatocladia* by Johansen[2]. Yendo[5], Manza[6], Segawa[7] and Kloezcova[8] presented basic anatomical information, whereas Murata[9] and Murata and Masaki[10] described and illustrated some of the reproductive organs.

The genus *Alatocladia* is segregated from *Calliarthron* by the presence of conceptacle primordia that are axial and marginal but never lateral, and from *Arthrocardia* by an intergenicular medulla in which the filaments are interlacing. Below we give the kind of basic structural information that will allow for a comparison of *Alatocladia* with these and other genera of coralline algae.

Materials and Methods

Specimens from Hakodate (Shinori), Hokkaido were fixed and decalcified in Susa fluid[11] and, after paraffin embedding and sectioning, stained with Delafield's hematoxylin and basic fuchsin, or sometimes phosphotungstic acid hematoxylin. Collections from the University of California, Berkeley (UC) were also examined for external features and conceptacle origin and eventual position.

Results

Vegetative Structure: Data on the dimensions of vegetative and reproductive features are given in the "Description" at the end of this section. Fronds mature enough to bear conceptacles arise in groups from crustose holdfasts. These holdfasts are comprised of several layers of filaments oriented approximately parallel to the substrate, the hypothallus, and a thicker layer of filaments arching upward and ending at the crust surface. This thicker part constitutes a perithallus of short plastid-containing cells and a layer of small epithallial cells.

The first intergenicula growing from holdfasts are small, barrel-shaped, and unbranched. As more intergenicula are produced distally they tend to be flat and lobed to varying extents (Figs. 1, 2). Their shape is a manifestation of meristematic activity at branch apices and at lateral surfaces. Also important in determining intergenicular morphology is branch and conceptacle production, and erosion. An intergeniculum unmodified by branching, conceptacles and erosion has distally projecting rounded lobes (Fig. 2). The intergenicula in a branch tend to lie in a single plane.

Branching in *Alatocladia modesta* is initiated when an apical meristem becomes divided into two or three (or sometimes more) parts, with continued growth leading to that number of branches. Branching is irregular, although some fronds become predominantly pinnate, as when an apical meristem divides into three parts with the central one growing fastest and so maintaining the branch axis.

The core of a branch consists of a group of medullary filaments with the apical cells of all the filaments comprising the terminal meristem (Figs. 5, 7). Branch elongation is due solely to the activity of this meristem in which the cells are all approximately the same length, unless in the process of division. Divisions occur more or less in synchrony, with waves of dividing cells resulting in tiers of

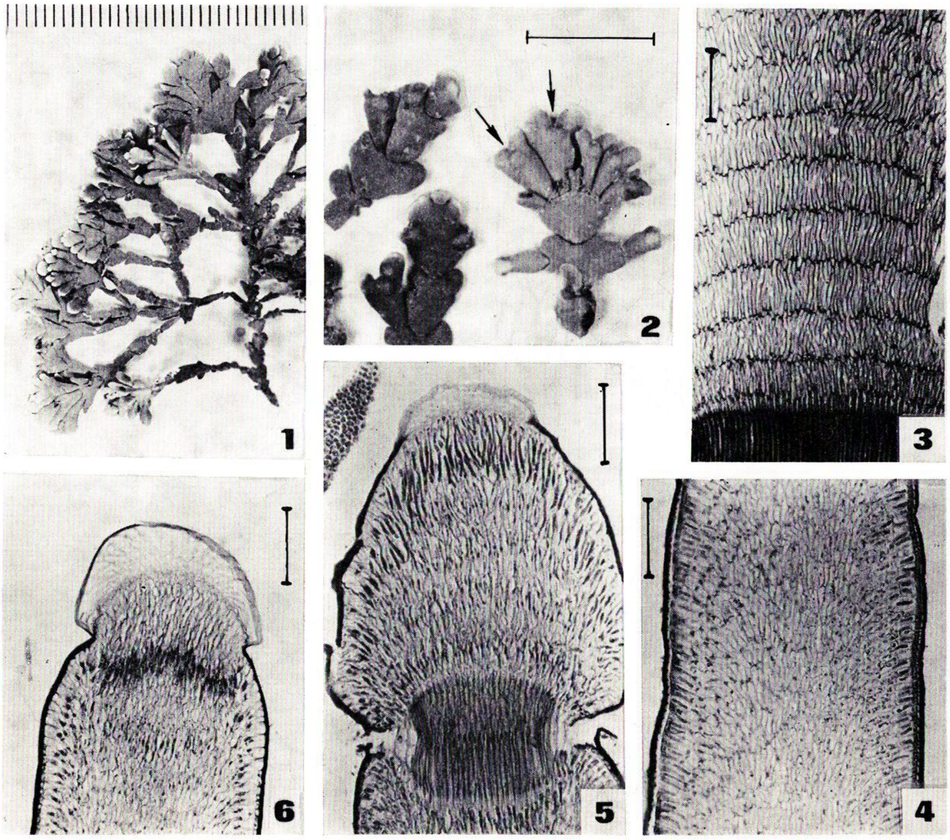

Fig. 1. Frond of *Alatocladia modesta* from Hakodate. Scale in millimeters.
Fig. 2. Part of branch with tetrasporangial conceptacles present (arrows). Scale=5 mm.
Fig. 3. Longisection through intergenicular medulla and part of a geniculum (below). Note that the medullary filaments are interlacing. Scale=100 μm.
Fig. 4. Longisection through young intergeniculum showing cuticle, epithallius and the intercalary meristem. Scale=100 μm.
Fig. 5. Longisection through branch showing expanded cuticle at the apex, the apical meristem and a young geniculum. Scale=100 μm.
Fig. 6. Longisection through branch apex fixed just as a geniculum was being initiated. The central parts of the genicular cells are beginning to take on the typical stainable condition which is probably indicative of uncalcified cell walls. Scale=100 μm.

medullary cells all about the same height (Fig. 3). During differentiation medullary cells become twisted, and only near genicula are they straight. It is not clear how this happens in cells that are encased in calcite. A meristem is separated from the ambient seawater by a layered cuticle which sometimes is blister-like over the apex; the blister may be filled with mucilage (Figs. 5–7).

At the flanks of branch apices the peripheral medullary cells arch laterally and become cortical tissue as branch elongation continues (Figs. 4–6). Cortices

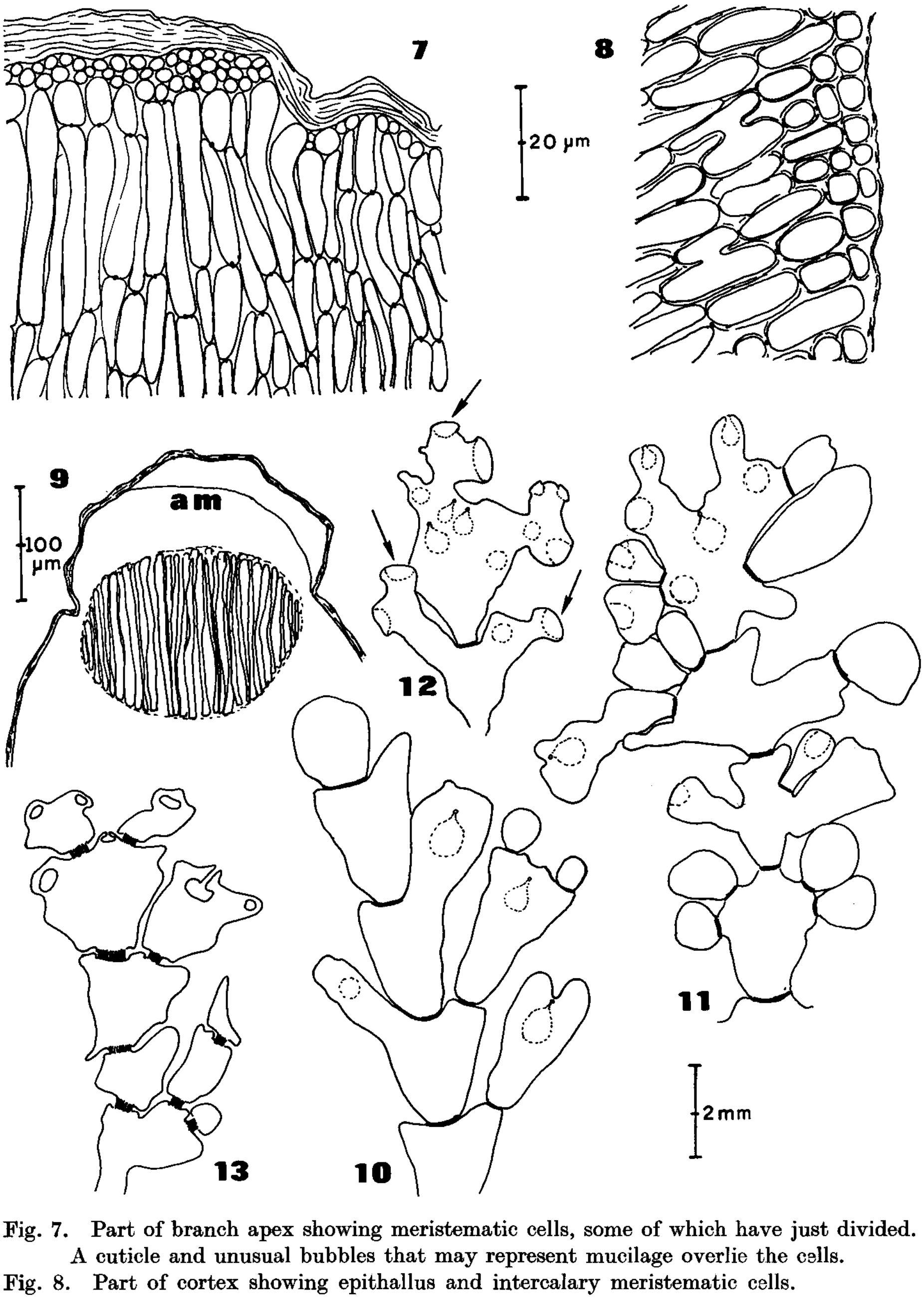

Fig. 7. Part of branch apex showing meristematic cells, some of which have just divided. A cuticle and unusual bubbles that may represent mucilage overlie the cells.

Fig. 8. Part of cortex showing epithallus and intercalary meristematic cells.

Fig. 9. Longisection through young geniculum that is directly below the apical meristem (am).

Fig. 10. Branch tip of tetrasporangial plant in which axial conceptacles were being produced in a regular manner.

are not tiered and consist of short cells containing plastids. The terminal cells of cortical filaments together constitute a prominent intercalary meristem that cuts off new cortical cells as well as short epithallial cells to the outside. An epithallus is usually one or two cell layers thick and covers all cortical surfaces (Figs. 4, 8); it does not extend over branch apices. A cuticle overlies the epithallus.

Periodically a terminal meristem produces a tier of medullary cells destined to become a geniculum. During genicular maturation (Figs. 5, 6, 9) the cells elongate as they become located farther below the apex; in contrast, intergenicular medullary cells do not elongate below the meristem. Also, the walls midway between the ends of the cells become more stainable, probably because of polysaccharide deposition. When the genicular cells are below the branch apex, the calcified cortex around the developing geniculum begins to show signs of destruction (Figs. 5, 6). Eventually there is a complete separation of the intergenicular cortex surrounding a geniculum. Local cell divisions result in flanges of calcified tissue extending all around a geniculum (Fig. 5). By the time a geniculum is fully developed, the genicular cells are much longer than intergenicular cells, with the uncalcified parts constituting most of this length.

Reproductive Structures: All conceptacles originate in medullary meristems either in axial or marginal locations (Figs. 10, 11). As in other corallinoidean taxa, conceptacle primordia are first recognized by the active secretion of a white cuticular cap which stains intensely in sectioned and hematoxylin-stained material (Figs. 14–16, 23, 28). In *A. modesta* a cap may be as much as 75 μm thick. Following cap formation the cells below appear to be in disorganized array, a phenomenon related to the cessation of growth in the fertile disc and continued growth all around the incipient chamber. The surrounding tissues lift the cap above the central area and continue to grow upward and centripetally so as to form a conceptacle roof (Fig. 16). The cap is eventually sloughed, usually after the roof and pore are partly developed. Early development is such that the pore is symmetrical along the long axis of the conceptacle, and the developing chamber, canal and pore are centrally located with respect to the fertile disc (Fig. 18). However, in tetrasporangial conceptacles, one lip or edge grows more rapidly than the other, and hence in mature conceptacles the pore is excentric, being located on one surface of the flat intergeniculum rather than at the upper edge directly above the chamber (Fig. 20). In sexual conceptacles the excentricity is less pronounced (Fig. 29) or even absent (Fig. 22).

During early stages of roof formation in tetrasporangial conceptacles small cells, the reproductive initials, develop on the fertile area. These cells are at first small but densely cytoplasmic (Fig. 24). As overarching growth of the roof continues, these cells enlarge until just prior to meiosis; they are more than 100 μm

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Fig. 11. Another tetrasporangial plant in which conceptacles were being produced in an irregular and proliferous manner.

Fig. 12. Part of a female plant showing the typical congested conceptacles and conceptacle primordia (arrows).

Fig. 13. Tracing of section of male branch. The irregular intergenicular outlines are because the section was not median for all intergenicula.

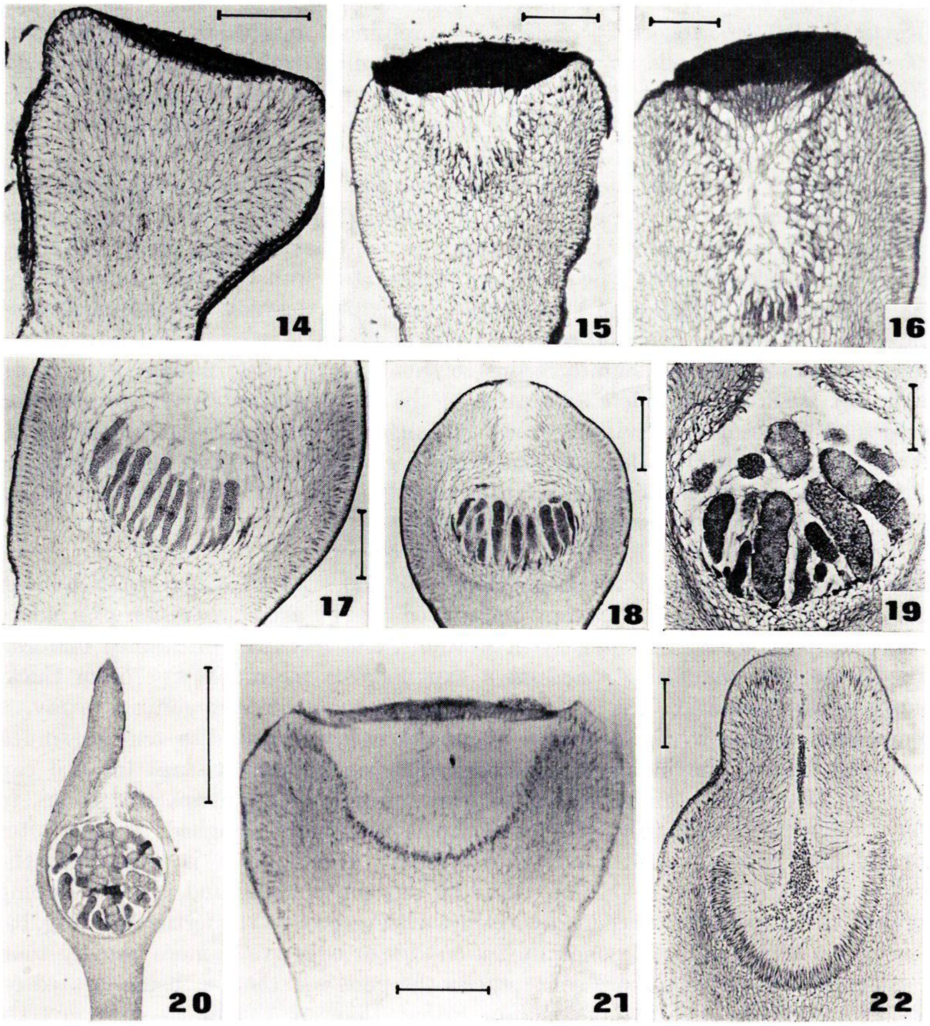

Fig. 14. Longisection through primordium of tetrasporangial conceptacle. Note the cap and the disorganized sub-cap space. Scale=100 μm.

Fig. 15. An older conceptacle in which tetrasporangial initials were originating at the time of fixation. Scale=100 μm.

Fig. 16. A more advanced stage of conceptacle formation in which young tetrasporangia are present. Scale=100 μm.

Fig. 17. Tetrasporangia just prior to meiosis. Scale=100 μm.

Fig. 18. A conceptacle fixed just after meiosis and during cytokinesis of some of the tetrasporangia. Scale=200 μm.

Fig. 19. A mature tetrasporangial conceptacle. Note the disrupted tissue surrounding the chamber. Scale=100 μm.

Fig. 20. Another fully developed tetrasporangial conceptacle. Note that one side of the conceptacle is extended and hence the pore opens on one intergenicular surface. Scale=500 μm.

long and each contains a conspicuous nucleus (Fig. 17). Sometime during early development, each sporangial initial divides and a sporangium comes to be subtended by a small stalk cell. Meiosis apparently occurs in the more centrally located tetrasporangia first and quickly results in a linear array of four nuclei in each enlarging sporangium (Fig. 19). Bisporangia were not seen.

In young stages of well-prepared conceptacles delicate, one or two-celled paraphyses were seen to occupy some of the cells of the fertile disc (Fig. 24). Hence the floors of tetrasporangial conceptacles are not covered by uniform layers of young tetrasporangia, but instead have a mixture of sterile and fertile cells.

The few male and female plants collected indicate that *A. modesta* is dioecious and that sexual plants are relatively rare. Like tetrasporangial plants, sexual conceptacles are axial or marginal in origin (Figs. 12, 13).

In male plants young conceptacles with caps still in place have a uniform layer of reproductive initials on the chamber floor (Fig. 21). Among these cells arise thin elongate paraphyses that extend more than 40 μm above the chamber floor (Fig. 21). They may function in mucilage secretion. Circumconceptacular growth results in a conceptacle with an elongate beak through the center of which passes the conceptacular canal (Fig. 22).

Longisections of mature conceptacles reveal bowl-shaped fertile areas roofed over by overarching filaments from around the chamber (Fig. 22). In most male conceptacles examined the pore was central with respect to the axis of the chamber.

The spermatangial initials cut off 1 to 3 spermatangial mother cells that, although small, form a dense layer in the bottom of the chamber. These cells begin to cut off spermatangia near the center of the fertile area even before the roof is fully formed. Although difficult to interpret with light microscopy it appears that upward extending processes arise from the spermatangial mother cells and become spermatangia. These processes elongate until by the time they are about as long as the paraphyses they separate from the mother cells (Fig. 25). Each spermatangium contains a nucleus and is drawn out in a long distal "tail" (Fig. 25). These "tails" appear devoid of contents and shrink until they virtually disappear. Large numbers of spermatangia cluster in the chamber and pass through the canal, probably in mucilage.

In female plants conceptacles are more crowded than they are in other reproductive types and as many as 11 per intergeniculum may be present (Fig. 12). Development may be excentric even early in development and by the time female conceptacles are mature, one lip of the tissue around the pore may extend more than the other (Fig. 29); however, the excentricity is not as pronounced as in tetrasporangial conceptacles.

The development of young conceptacles from primordia is apparently the same as for other reproductive types except that the initials develop into procarps. A

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Fig. 21. Longisection through young male conceptacle. Spermatangial mother cells constitute the deeply staining layer on the chamber floor and above them extend the paraphyses. Scale=100 μm.

Fig. 22. Median section through a male conceptacle producing spermatangia. Scale=100 μm.

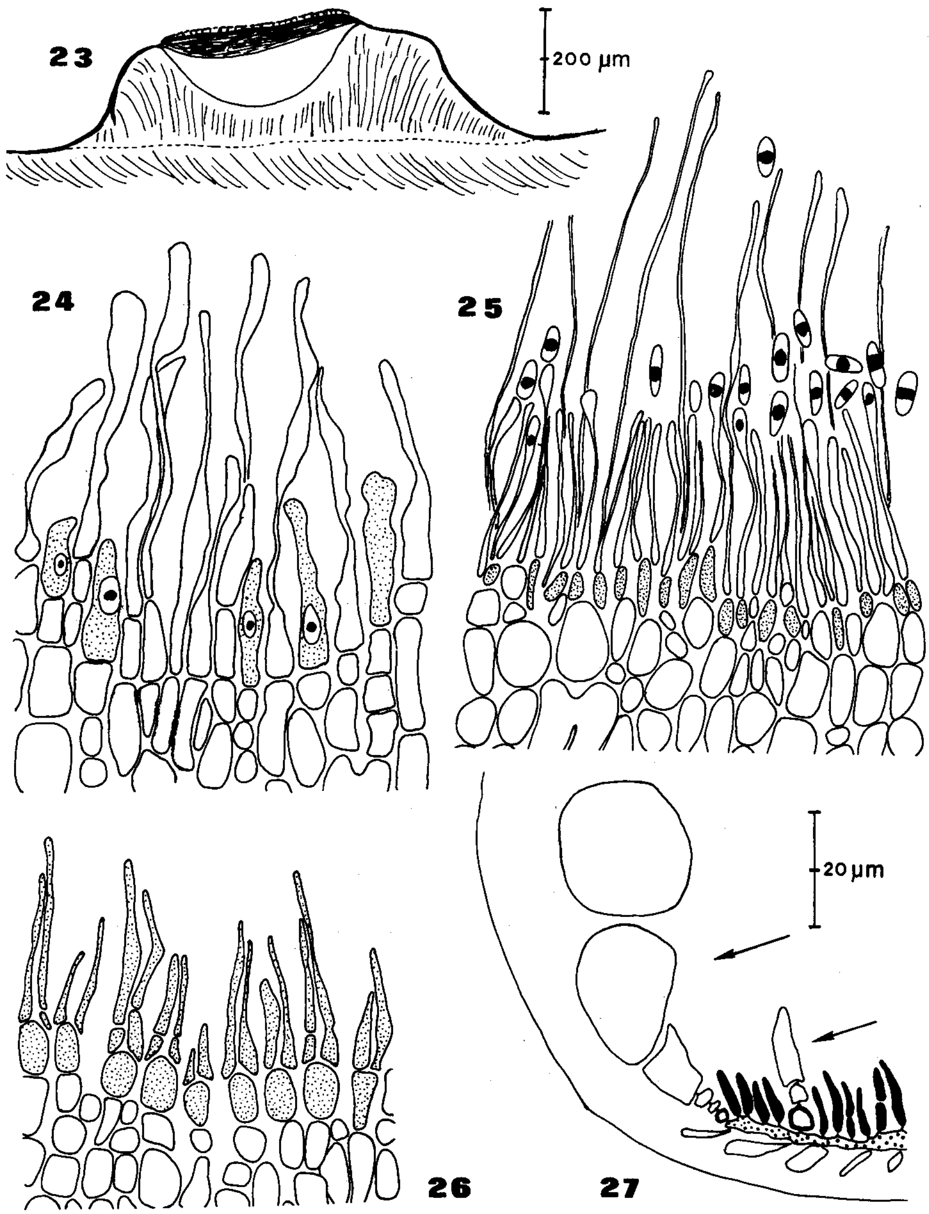

Fig. 23. Section through the only lateral conceptacles encountered; it is male. Probably the conceptacle would have become pseudolateral and projected strongly from the surface of the intergeniculum.

Fig. 24. Enlargement of some young tetrasporangia in a conceptacle like the one in Figure 16.

Fig. 25. Part of fertile area in a male conceptacle. The spermatangial mother cells are stippled and the spermatangia contain nuclei.

uniform layer of young procarps is present at an early stage of development, sometimes even before the cap has sloughed off (Fig. 28). In the conceptacle in Figure 28 there is evidence of amorphous material between the bottom of the cap and the procarps; this is possibly mucilage. Throughout the fertile disc on the conceptacle floor there are one or two carpogonial filaments per supporting cell; two are shown in Figure 26. At first the procarps are two-celled, with each distal cell differentiating into a long trichogyne and then dividing transversely so as to form a carpogonium and a small hypogynous cell (Fig. 26). Procarps near the periphery of the discs usually do not form trichogynes nor hypogynous cells. At maturity the trichogynes extend through the conceptacle canal (Fig. 29).

Following presumed fertilization trichogynes degenerate and the supporting cells amalgamate into a thin, broad fusion cell that is mostly coherent over the floor of the conceptacle (Figs. 27, 30, 31). During this time the chamber broadens considerably and continued growth of surrounding vegetative tissue sometimes results in deeply embedded conceptacles. Degeneration of the carpogonial filaments continues until each is represented by a single cell containing what appears to be disorganized nuclear material (Fig. 27). Meanwhile gonimoblast filaments begin to grow from the surface and margin of the fusion cell, with a characteristic pedestal-like cell at the base of each filament (Fig. 27). It is not clear how divisions occur to cut off the cells of gonimoblast filaments, but it may be from this basal cell. The new cells enlarge markedly until

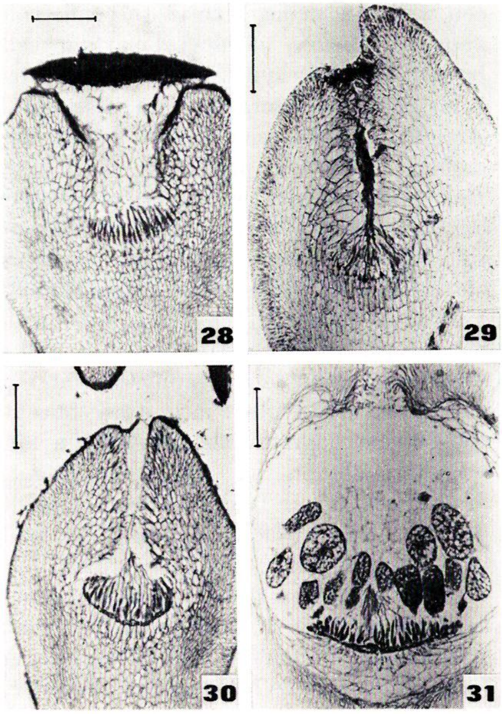

Fig. 28. A young female conceptacle with the cap still in place. Scale=100 μm.
Fig. 29. An older female conceptacle in which excentric growth is becoming evident. The deeply staining mass in the conceptacular canal are trichogynes. Scale=100 μm.
Fig. 30. A young cystocarpic conceptacle in which a fusion cell has formed but in which gonimoblast filaments are not present. Scale=100 μm.
Fig. 31. A fully developed cystocarp. Scale =100 μm.

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Fig. 26. Procarps in a young female conceptacle.
Fig. 27. Gonimoblast filaments (arrows) arising from the margin and upper surface of a fusion cell (stippled). The pedestal-like basal cells are darkly outlined. The remains of the carpogonial filaments are black.

the terminal cells may be as much as 80 μm in diameter. These large cells are the carposporangia; they presumably release their contents as carpospores.

Description of Alatocladia modesta: *Holdfasts*: crustose; *Fronds*: up to 6 cm high, flattened in the upper parts; *Branching*: pinnate and dense, less often dichotomous or irregular; *Intergenicula*: near base terete and barrel-shaped, in upper parts flat but otherwise variable in shape, mostly 1–4 mm long, 1–4 mm broad, distal paired lobes often present, usually rounded; *Genicula*: single cellular tiers, cell walls uncalcified except the ends calcified and embedded in the intergenicula above and below, uncalcified parts of cells 150–300 μm long, genicula 140–400 μm broad; *Medulla*: synchronous apical growth resulting in 30–40 tiers of intergenicular cells per intergeniculum, tiers 45–70 μm high, cells mostly interlaced, but straight close to genicula and below conceptacles; *Cortex*: made up of filaments arching from the peripheral medullary cells, cells pigmented, 6–25 μm long; *Epithallus*: one (or two) layers of cells covering all calcified surfaces, cells 3–9 μm long and 5–8 μm broad, the outer walls uncalcified and densely staining; *Conceptacles*: axial or marginal in origin, one to several developing in the apices or margins of terminal or subterminal intergenicula, often becoming deeply embedded and protruding little on the flat intergenicular surfaces; *Tetrasporangial conceptacles*: fertile surfaces on concave floors as well as walls of chambers, young conceptacles containing delicate paraphyses interspersed among tetrasporangial initials, paraphyses not evident in mature conceptacles, chambers 380–480 μm in diameter, 450–600 μm high, canals 130–300 μm long, curved so pores open subapically or submarginally on flat surfaces of intergenicula, tetrasporangia 150–190 μm long; *Male conceptacles*: beak-like roofs present, but not as pronounced as in related genera, fertile surfaces on floors and walls of chambers, paraphyses 40–110 μm long, chambers 200–450 μm in diameter, canals 300–450 μm long; *Female conceptacles*: chambers 100–230 μm in diameter, floors covered with supporting cells, each producing 1–2 carpogonial filaments; *Carposporangial conceptalces*: chambers 380–500 μm in diameter, 320–500 μm high, canals 150–300 μm long, fusion cells thin, 7 μm thick and 200–350 μm in diameter, often perforate, gonimoblast filaments arising from margin and upper surface of fusion cells, mature carposporangia 70–90 μm in diameter.

The dimensions given above are a synthesis of our measurements and those given in Yendo[3], Murata[9] and Murata and Masaki[10]. They give the usual ranges, but exclude unusually low or high figures that are sometimes obtained.

Discsusion

The research presented in this survey of the general features of *Alatocladia modesta* brings up questions that cannot be answered until more precise studies can be made. The cells in terminal meristems are more or less straight, but the differentiated intergenicular medullary cells are twisted. During the transition from meristematic to medullary cells this transformation occurs. (Near genicula the medullary cells remain straight.) Presumably calcium carbonate is deposited in cell walls while they are still part of the meristem. If so, how do the cells assume their contorted appearance? This phenomenon occurs also in *Calliarthron*,[2),4)] but not in other related genera (e.g., *Bossiella*).

A cuticle covers all calcified surfaces, but over the branch apices it was often separated from the underlying meristem by what might be mucilage. This is unusual, although the cuticle has been reported to be thicker over branch apices than on lateral surfaces (in *Corallina*, *Bossiella*, and *Calliarthron*)[12)]. The "blistering" in *Alatocladia* may be related to active growth in the terminal meristem.

Genicula originate when a special medullary tier develops differently from the more usual medullary tiers comprising intergenicula. The cells in the genicular tier continue elongating even as more medullary tiers are produced by the terminal meristem. This elongation occurs when cell walls, probably made up of polysaccharides, grow midway between the cell ends. The newly deposited material is uncalcified and stains intensely. As genicular elongation continues the surrounding calcified cortex, which is not part of the geniculum, becomes disorganized and splits apart. Hence the geniculum becomes exposed. This is apparently developmentally identical to genicular maturation in other genera in the subfamily Corallinoideae[2)].

Unlike the closely related *Calliarthron*[2)], conceptacles do not originate in cortical tissue in *Alatocladia*. (In all the specimens we examined only one cortical conceptacle was found; it is illustrated in Figure 23.) In *A. modesta* the conceptacles originate in medullary tissues, many of them being axial and in line with subtending genicula. When used in generic diagnoses features like conceptacle origin should be restricted to tetrasporangial plants, because in sexual plants conceptacles are sometimes crowded and their type of origin sometimes unclear. The excentricity of the conceptacle pore appears to be universal in *Alatocladia*, but, again, as a diagnostic feature only tetrasporangial conceptacle should be used. We are unable to indicate whether pore excentricity is related to a dorsiventral orientation of branches in the field; this is perhaps possible. Excentric pores in medullary conceptacles have also been reported for two species of *Arthrocardia*, *A. duthiae* Johansen[2)] and *A. silvae* Johansen[13)]. But, in this genus this characteristic is taxonomically useful only at the specific level; most species of *Arthrocardia* have central pores. Conceptacles in *Chiharaea bodegensis* Johansen[14)] also have pores opening excentrically, but here they have been shown to be located on the upper surfaces of dorsiventrally oriented branches.

Paraphyses growing among young tetrasporangia have been reported for several species, for example, *Bossiella cretacea* (Post. et Rupr.) Johansen[15)] and *Calliarthron yessoense* (Yendo) Manza[16)]. However, they are absent in *Calliarthron tuberculosum*[2)]. Murata and Masaki[10)] reported them in *A. modesta*, and we have verified their presence. It might be that tetrasporangial paraphyses are more prevalent in the Corallinoideae than hitherto recognized. They are, however, absent in the tribe Janieae[17)]. Paraphyses in male conceptacles have also been reported in *C. tuberculosum*[2)] and they may play a role in mucilage secretion, or they may in some other way facilitate sperm production and dispersal.

Alatocladia modesta can be added to the list of coralline algae in which gonimoblast filaments arise from the margins and also from the upper surfaces of fusion cells[18)]. Closely related genera in which this occurs are *Calliarthron*[2)], *Bossiella*[19)] and *Arthrocardia*[20)].

With this presentation of basic structural features of *A. modesta* all of the genera of the Corallinoideae have been surveyed. Many questions remain, however, and hopefully some of these can be answered as more precise and sophisticated techniques can be applied. Important structural data may also become available when ecological studies can be coupled with anatomical and morphological studies. The influence of environment on structure is little known in articulated coralline algae.

Acknowledgements

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