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Developmental morphology of *Chondrus crispus* (Gigartinaceae, Rhodophyta)

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The vegetative and reproductive development of the type species of *Chondrus*, *C. crispus* Stackhouse (Gigartinaceae, Rhodophyta), is described based on material from Britain and Ireland. *Chondrus* is distinguished from other members of the Gigartinaceae primarily by the absence of enveloping secondary filaments in the cystocarp. The procarp of *C. crispus* is typical for members of the Gigartinaceae and functional auxiliary cells form numerous enucleate protrusions, each of which potentially cuts off a gonimoblast initial. Gonimoblast filaments are narrow, uninucleate and resemble the connecting filaments found in non-procarpic families of red algae. Only the apical gonimoblast cells are densely filled with cytoplasm, the rest being highly vacuolate. Medullary cells are transformed into nutritive and potential generative cells as the gonimoblasts ramify through the medulla. The nuclei in each medullary cell undergo mitosis simultaneously, followed by protein synthesis and breakup of the central vacuole. Intercalary gonimoblast cells link progressively with the swollen, transformed medullary cells by means of secondary pit connections, and transfer a diploid nucleus. Both gonimoblast cells and heterokaryotic medullary cells bear carposporangia in short chains. Other gonimoblast filaments penetrate the cortex, causing gaps in the surface layer through which the carpospores are released, or produce secondary carposporangial filaments or are involved in tissue repair. Tetrasporangia are formed entirely in secondary filaments derived from medullary cells that cross-link to medullary cells in other filaments, forming secondary pit connections. Tetraspores are released through multiple pores in the outer layer of the sorus, and the tissue is subsequently repaired. A revised description of *Chondrus* is provided and the relationship of North Atlantic *C. crispus* to species of *Chondrus* from the western North Pacific is discussed.

INTRODUCTION

Chondrus crispus Stackhouse, the type species of *Chondrus* Stackhouse (1797), is a common intertidal species on both sides of the North Atlantic Ocean (South & Tittley 1986) and, along with *Mastocarpus stellatus* (Stackhouse) Guiry, is harvested commercially in France and Canada for its carrageenans (McLachlan 1985; Briand 1991). Until recently, *C. crispus* has also been regarded as occurring in Japan (e.g. Mikami 1965). Lüning *et al.* (1986), however, demonstrated that thalli of *Chondrus crispus* from Japan have a temperature survival limit 1–2°C higher than those from the North Atlantic, that the two do not cross in culture, and that they differ in morphology. Detailed life-history and morphological studies (Brodie *et al.* 1991) confirmed these observations, and the Japanese plants formerly treated under *C. crispus* were referred to *Chondrus nipponicus* Yendo.

Chondrus Stackhouse, *Iridaea* Bory, *Rhodoglossum* J. Agardh and *Gigartina* Stackhouse were placed together in the tribe Gigartineae by J. Agardh (1876, pp. 175–176) and presently compose the family Gigartinaceae (Guiry & Garbary 1990). J. Agardh (1876, pp. 175–178) distinguished *Chondrus* from the other three genera on the basis that the 'nucleus' of the cystocarp is subindefinite in extent, and not constrained at its boundary by a filamentous network. Kim (1976, pp. 36–46) recognized only two genera in the Gigartinaceae. He retained *Chondrus*, including *C. crispus* and a few species from the northwestern Pacific that lacked an enveloping tissue around the gonimoblasts, and placed all other species in the genus *Gigartina*.

Cystocarp morphology of *Chondrus crispus* was investigated by Kylin (1923, pp. 19–22) and Kim (1976, pp. 32–33), and Mikami (1965, pp. 220–259) described and illustrated gonimoblast filaments ramifying through the medulla and linking to individual medullary cells in species of *Chondrus* from Japan.

As part of a continuing effort to characterize properly the genera of the Gigartinaceae (Hommersand *et al.* 1992), we here document the vegetative and reproductive morphology of the type species of *Chondrus, C. crispus*. Special emphasis is placed on the development of the gonimoblast filaments and their interactions with transformed medullary cells; a revised description of the genus *Chondrus* is provided.

METHODS

Plants investigated in this study were fixed in the field in 10% Formalin/seawater within 30 min after collection, drained after 24 h and stored in 5% Formalin/seawater. Material selected for examination was placed under a 40-W tungsten lamp in 5–10% Formalin/seawater for at least a week prior to sectioning, or until bleached completely white. Periclinal, longitudinal and transverse sections were made by hand using a platinum-chrome double-edged razor blade. Sections were stained either with aceto-iron-haematoxylin-chloral hydrate (Wittmann 1965) for a period ranging from 30 min to 4 h and mounted in 1 : 1 Hoyer's medium : distilled water according to the procedure of Hommersand *et al.* (1992), or were stained and mounted in a mixture of 1% aqueous aniline blue in 1 : 1 distilled water : KARO® corn syrup. Photographs were taken with a Zeiss Photomicroscope III using T-MAX Kodak film. Herbarium abbreviations follow those of Holmgren *et al.* (1990).

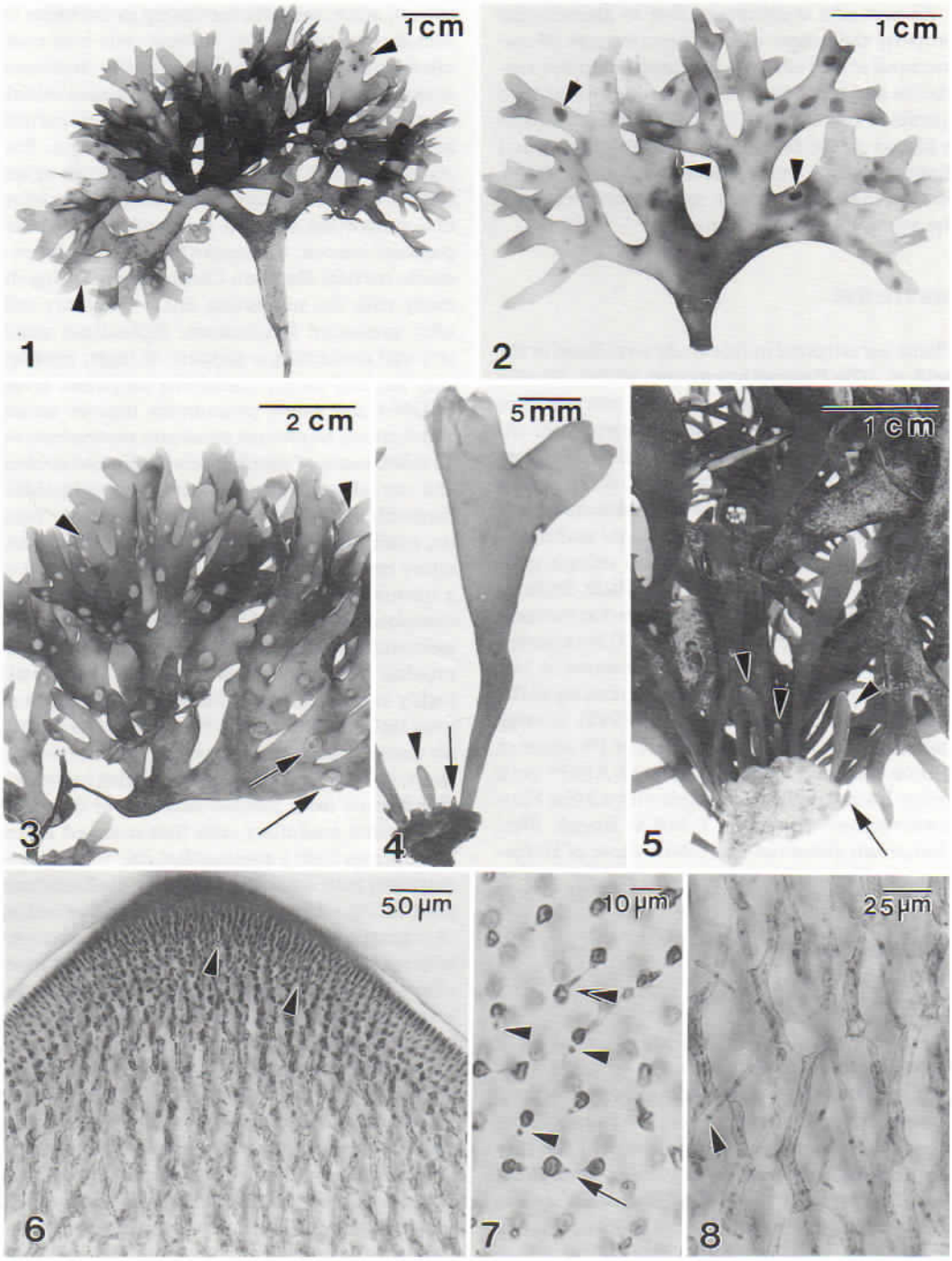
OBSERVATIONS

Chondrus Stackhouse 1797: xv

DESCRIPTION: Thallus growing attached by a discoid holdfast from which few to many subcylindrical stipes arise, expanding gradually into compressed or flattened, more or less dichotomously branched erect blades; marginal and surface proliferations present in some species. Erect blades growing by a marginal meristem that is either restricted to the tips of branches or extends along the sides of blades; cortex more or less constant at 6–7 cell layers thick; medulla composed of a network of primary filaments interconnected by secondary pit connections and numerous secondary filaments 1–2(–3) cells long, linked terminally by secondary pit connections to other primary or secondary medullary cells or to each other; medulla increasing in thickness by transformation of inner cortical cells into medullary cells. Gametophytes generally dioecious, occasionally monoecious. Spermatangial initials formed in small patches from surface cortical cells, each cutting off 1(–2) spermatangia. Procarps formed within the meristem from apical initials of leading cortical filaments, consisting of a supporting cell and a curved, 3-celled carpogonial branch; the supporting cell also bears a sterile cortical filament. Carpogonium fusing directly with the supporting cell (= auxiliary cell) after presumed fertilization; diploidized auxiliary cell containing a mixture of large, presumably haploid nuclei containing amplified levels of DNA and small, presumably diploid nuclei, and forming numerous enucleate protrusions on all sides, some of which receive a diploid nucleus and cut off a gonimoblast initial; gonimoblast filaments radiating laterally and inwardly from the auxiliary cell, penetrating between the medullary cells, each filament growing by means of a narrow apical cell that is densely filled with cytoplasm and branching from a cytoplasm-rich subterminal gonimoblast cell; intercalary gonimoblast cells narrow, uninucleate, and mostly highly vacuolate, some linking to enlarged, multinucleate medullary cells by means of secondary pit connections; carposporangial initials borne in short, unbranched or branched chains issuing either directly from gonimoblast cells or from heterokaryotic medullary cells that received a diploid nucleus from a gonimoblast cell, uninucleate, maturing into carposporangia, or multinucleate after fusing with conjunctor cells and reverting to vegetative cells. Cystocarps circular to ovate, without an ostiole, and lacking secondary medullary or enveloping filaments; carpospores released through gaps in the outer cuticle, which are subsequently repaired. Tetrasporangial sori non-protruding, irregular in shape and size; tetrasporocytes generated in short chains formed secondarily from medullary cells, either in the centre or towards the outer edges of the medulla, the ends free or cross-linked terminally to medullary cells in separate filaments by terminal secondary pit connections; tetrasporangia with cruciately to irregularly arranged spores, released through pores in the outer cuticle, followed by tissue repair.

ETYMOLOGY: From the greek *chondros*; refers to the cartilaginous nature of the dried thallus.

SYNONYM: *Polymorpha* Stackhouse (1816, p. xi), *pro parte*.



Figs 1–8. *Chondrus crispus*. *Figs 1–5*. Habits (NCU).

Fig. 1. Gametophyte bearing young cystocarps (arrowheads). Cuckmere Haven, Sussex, UK (*Maidment*, 29.ix.1991).

Fig. 2. Tetrasporangial plant bearing sori. Cuckmere Haven, Sussex, UK (*Maidment*, 29.ix.1991). (Arrowheads indicate sori of similar age.)

Fig. 3. Female gametophyte bearing young (arrowheads) and old (arrows) cystocarps. Cuckmere Haven, Sussex, UK (*Maidment*, 29.ix.1991).

TYPE SPECIES: *Chondrus crispus* Stackhouse.

***Chondrus crispus* Stackhouse (1797, p. xxiv)**

NOMENCLATURAL HISTORY: *Chondrus crispus* Stackhouse, the type species of the genus (Schmitz 1889, p. 440), was originally based on *Fucus crispus* Linnaeus (1767, p. 134), a later homonym of *Fucus crispus* Hudson (1762, p. 472), [= *Phyllophora crispa* (Hudson) Dixon (Dixon 1964, p. 56)]. *Fucus crispus* Linnaeus is thus a *nomen illegitimum* (see Papenfuss 1950). Papenfuss (1950, p. 191) pointed out that *Chondrus crispus* Stackhouse is thought to have first been described by Hudson (1762, p. 472) under the name *Fucus filiformis*, but that 'The specific epithet cannot be transferred to *Chondrus*, since Okamura and Segawa (in Segawa 1935, p. 81) have described a species of *Chondrus* under the name *Chondrus filiformis*'. This latter entity is actually *Gigartina tenella* Harvey 1859 (see Mikami 1965, p. 208). According to Art 72, note 1, International Code of Botanical Nomenclature (Greuter 1988), the name *Chondrus crispus* Stackhouse can be retained without Linnaeus in parenthesis (Papenfuss 1950).

HOLOTYPE: LINN 1274.68.

TYPE LOCALITY: Atlantic Ocean; precise locality unknown.

SYNONYMS:

Fucus crispus Linnaeus (1767, p. 134) nom. illeg. non *F. crispus* Hudson (1762, p. 472)
Fucus ceranoides S.G. Gmelin (1768, p. 115) non *F. ceranoides* Linnaeus (1753, p. 1158)
Fucus membranifolius Withering (1796, p. 106)
Fucus lacerus Stackhouse (1797, p. xxiv)
Fucus polymorphus Lamouroux (1805, p. 1)
Ulva crispa (Linnaeus) de Candolle (1805, p. 13)
Chondrus polymorphus (Lamouroux) Lamouroux 1813, p. 39)
Fucus crispatus Lyngbye (1819, p. 15)
Sphaerococcus crispus (Linnaeus) C. Agardh (1820, p. 24)
Chondrus incurvatus Kützing (1843, p. 399)

REPRESENTATIVE SPECIMENS EXAMINED: Lower intertidal, Sidmouth, Devon, England, UK (*Brodie*, 5.v.1991, monoecious: cystocarpic and male, tetrasporangial, NCU); Lilstock, Somerset, England, UK (*Brodie*, 27.ii.1991, cystocarpic, NCU); Cuckmere Haven, Sussex, England, UK (*Maidment*, 29.ix.1991, cystocarpic, tetrasporangial); Spanish Point, County Clare, Ireland (*Hommersand*, 2.vii.1985, cystocarpic, tetrasporangial, NCU).

DISTRIBUTION: Amphi-atlantic. *Eastern Atlantic*: throughout Britain and Ireland, Iceland, Norway to southern Spain, and possibly Morocco and the Cape Verde Islands. *Western Atlantic*: from Newfoundland, Canada, to Delaware, USA (Dixon & Irvine 1977; South & Tittley 1986).

HABITAT: Epilithic, from upper intertidal pools to 24 m subtidally, in shelter and areas exposed to some wave action (Dixon & Irvine 1977).

HABIT: Adult plants of *Chondrus crispus* are typically 5–7 times dichotomously branched, variable in width and thickness (Figs 1–3). Branchlets are sometimes proliferous from the margins (Fig. 5). Attachment is by a perennial crustose holdfast that gives rise periodically to cylindrical, erect juvenile thalli 0.5–1.0 mm tall which develop into flattened dichotomous erect blades (Figs 4–5).

Young cystocarps form near the apex of female plants (Fig. 1) and often remain intact throughout the growing season (Fig. 3). New tetrasporangial sori are initiated near the apices or along the thallus margin (Fig. 2).

VEGETATIVE DEVELOPMENT: The apex of a juvenile upright under 1 mm tall is cylindrical with a dome-shaped apex (Fig. 6). A slightly oblique longitudinal section through the apex reveals an abundance of conjunctor cells issuing from intercalary cells just below the thallus surface (Fig. 6). As seen in a transverse section (Fig. 7), a conjunctor cell cut off from an intercalary cell fuses horizontally with a cell in an adjacent fil-

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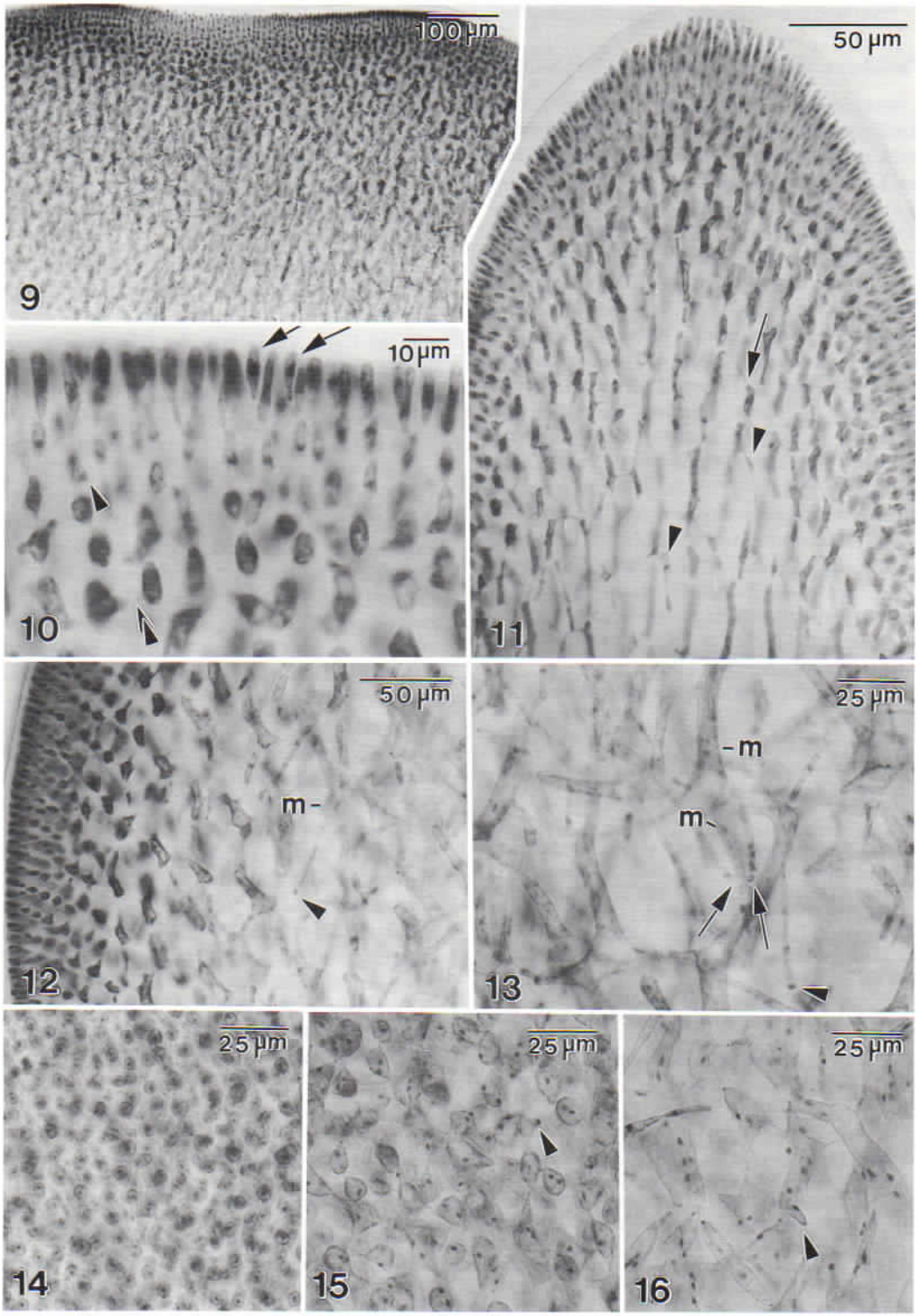
Fig. 4. Crustose holdfast bearing terete (arrow) and flattened juvenile upright (arrowhead), and young dichotomizing foliose thallus. Lilstock, Somerset, UK (*Brodie*, 27.ii.1991).
Fig. 5. Crustose holdfast bearing mixture of terete (arrow) and flattened (arrowheads) juvenile uprights, and adult thalli with marginal proliferations. Lilstock, Somerset, UK (*Brodie*, 27.ii.1991).
Figs 6–8. Vegetative development of terete juvenile upright. Sidmouth, Devon, UK (*Brodie*, 5.v.1991).
Fig. 6. Oblique periclinal section. Apical region showing abundance of conjunctor cells (arrowheads) and zigzagging medullary cells.
Fig. 7. Transverse section just below apex. Conjunctor cells (arrowheads) cut off from intercalary cells, fusing (double arrowhead) with nearby cell forming a secondary pit connection (arrow).
Fig. 8. Detail of medulla from specimen in Fig. 6 showing medullary cells cutting off narrow, elongated cells bearing terminal conjunctor cells (arrowhead).



Figs 9–16. *Chondrus crispus.* Vegetative system. Sidmouth, Devon, UK (*Brodie*, 5.v.1991, NCU). *Figs 9–11.* Flattened juvenile upright 1 cm high.

Fig. 9. Median periclinal section of apex with incipent dichotomy.

ament, forming a secondary pit connection. The donor cell sits next to the incipient pit plug and the recipient cell is provided with a lateral extension formed by the flow of cytoplasm into the fused conjunctor cell. The thallus expands, revealing a primary network in which every cell is connected to each adjoining cell in the same filament by a primary pit connection and to every neighbouring cell in an adjacent filament by a secondary pit connection. A short distance behind the apex, the thallus differentiates into a cortex composed of subspherical cells 6–7 cell layers thick and a medulla of longitudinally elongate cells that are nearly uniform in diameter and zig-zag in shape, linked by secondary pit connections (Figs 6, 8). Medullary cells generate initials from their lower sides that grow downwards at an angle through the intercellular matrix and cut off conjunctor cells terminally that form secondary pit connections with nearby medullary cells below (Fig. 8). Such interlinking secondary filaments are seldom more than one cell long.

Upright juvenile axes more than 0.5 mm tall rapidly expand in one plane, becoming compressed or flattened (Fig. 4). The apical meristem extends laterally across the broadening tip and down the margin and surface of the thallus over a short distance (0.5–1.0 mm). Tips that have begun to branch dichotomously are surmounted by two dark-staining meristematic areas separated by a lighter region in which cell divisions and the formation of lateral conjunctor cells has slowed or ceased (Fig. 9). Meristematic apical cells are approximately twice as long as broad after cell division. Each apical cell elongates and typically undergoes a longitudinal concavo-convex division followed by a second transverse division in a pattern that leads to pseudodichotomous branching. Additional transverse divisions occur infrequently in actively growing meristems, and unbranched cells are uncommon. The first of any pair of apical initials is usually cut off adaxially and contributes filaments to the weakly defined central axis; the second apical initial is typically abaxial and generates the diverging filaments that form the cortex (Fig. 10). The medulla is densely filled with stellate cells as seen in periclinal section (Fig. 9) and is looser, composed of narrow, elongated cells when viewed in longitudinal section (Fig. 11). Ten to fifteen cells below the apex, the medullary cells protrude from their lower sides and cut off initials which elongate to form narrow secondary filaments that are mostly one cell long. Each secondary filament cuts off a conjunctor cell terminally that links to a medullary cell, usually in a separate cell row below, forming a secondary pit connection (Figs 11–13). In this way, the space between cells of the expanding primary network is filled progressively by one-celled secondary filaments attached to primary medullary cells and to each other. Such filaments are abundant and form intricate networks in older, more cartilaginous parts of the thallus.

The meristem may extend 0.5 to 1.0 mm below a narrow or broad apex, but is not diffuse in *Chondrus crispus*. Adventitious branches, when present, arise secondarily from surface cells along the margin below the meristematic region. Surface cells lack secondary pit connections and are uninucleate (Fig. 14). Inner cortical cells are connected by secondary pit connections and are multinucleate (Fig. 15); outer medullary cells are stellate in shape, and interconnected by secondary pit connections and one-celled secondary filaments. Nuclei increase in number in medullary cells as long as growth is taking place; however, there appears to be a close correlation between the number of nuclei and the number of secondary pit connections in any one cell. No instance of nuclear divisions was seen that was not associated with the formation of secondary pit connections in vegetative tissues. Once formed, the cortex remains constant at about 6–7 cell layers

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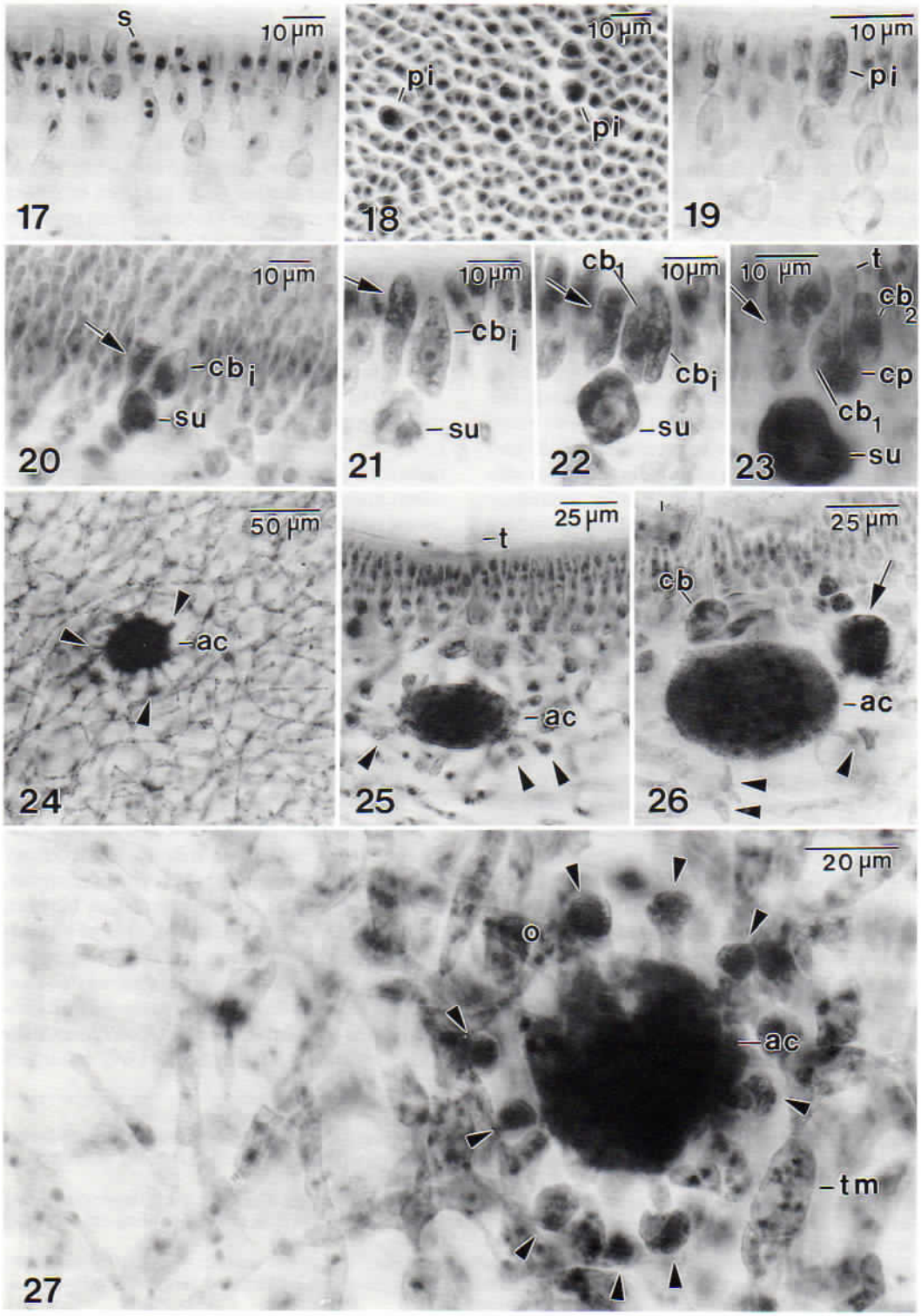
Fig. 10. Median periclinal section of apex showing undivided apical cells and apical cells divided longitudinally by concavo-convex septa (arrows). Subapical cells cut off conjunctor cells (arrowhead) forming secondary pit connections (double arrowhead).

Fig. 11. Longitudinal section of apex showing apical cells, radiating cortical filaments, medullary cells cutting off narrow secondary cells (arrowheads) which fuse (arrow) by conjunctor cells to neighbouring cells forming secondary pit connections.

Figs 12–13. Median periclinal section through cortex and medulla (Fig. 12) and medulla (Fig. 13) 0.5 mm below apex. Medullary cells bear narrow, descending secondary cells which cut off terminal conjunctor cells (arrowheads) that fuse (arrows) with neighbouring medullary cells.

Figs 14–16. Three periclinal focal points through cortex and medulla 0.5 mm below apex showing uninucleate surface cells (Fig. 14), mostly binucleate subcortical cells cutting off conjunctor cells (arrowhead) (Fig. 15) and multinucleate, irregularly elongated medullary cells initiating secondary filaments (arrowhead) (Fig. 16).



Figs 17–27. *Chondrus crispus*. Male (Fig. 17) and pre- and early post-fertilization female (Figs 18–27) reproductive systems. Sidmouth, Devon, UK (*Brodie*, 5.v.1991, NCU).

in thickness (Fig. 12), and any increase in thallus breadth or thickness is brought about through transformation of inner cortical cells into medullary cells within the meristematic region, as new files of cortical cells are interpolated at the thallus surface.

MALE REPRODUCTION: Male thalli were absent in our collections. A few cystocarpic plants from Sidmouth, Devon, contained small patches of elongate surface cells near the apex that appeared to function as spermatangial initials. Each spermatangial parent cell cuts off 1(–2) uninucleate spermatangia by an oblique to nearly transverse septum (Fig. 17).

FEMALE REPRODUCTION: The procarp consists of a supporting cell and a 3-celled, horizontally curved carpogonial branch; a vegetative cortical filament is also borne on the supporting cell (Fig. 23). Procarps are initiated at the thallus surface within the meristematic region up to 1 mm behind the apex. Procarp initials and young procarps are easily distinguished in surface view, in that they consist of darkly staining, uninucleate cells 2–3 times the diameter of ordinary surface cells (Fig. 18). Each procarp initial corresponds to the apical cell of a leading cortical filament (Fig. 19). It divides obliquely by two concavo-convex septa to produce an intercalary cell (the supporting cell), an adaxial terminal cell (the initial of the carpogonial branch), and an abaxial terminal cell (the initial of a cortical filament) (Figs 20, 21). The initial of the carpogonial branch divides further by a longitudinal septum into an apical and an intercalary cell (Fig. 22). The apical initial, in turn, cleaves by a curved septum oriented approximately perpendicular to the previous division to produce the terminal carpogonium. Finally, the tip of the carpogonium extends towards the thallus surface forming a terminal, club-shaped trichogyne (Fig. 23) which does not extend much beyond the surface of the thallus. The initial of the lateral sterile filament of the procarp divides pseudodichotomously in the same manner as a vegetative cortical filament. At maturity, the carpogonium usually lies between the first and second cell of the carpogonial branch at a right angle to the plane passing through the supporting cell, the first and second cells of the carpogonial branch, and the sterile procarpial filament (Fig. 23).

Cells of the procarp remain uninucleate up to the stage of trichogyne initiation (Figs 19–22). As the procarp reaches maturity, the supporting cell enlarges and becomes multinucleate, and the base of the carpogonium is seen extending towards the supporting cell (Fig. 23). Surface cortical cells surrounding the young procarp divide 2–3 times, so that the supporting cell of the mature procarp lies 2–3 cell layers below the thallus surface.

Fertilization was not observed. After presumed fertilization, the carpogonium evidently fuses directly with the supporting cell, depositing the diploid nucleus. The supporting cell functions as an auxiliary cell.

CARPOSPOROPHYTE DEVELOPMENT: The auxiliary cell continues to enlarge after diploidization, becoming subspherical in shape and filled with

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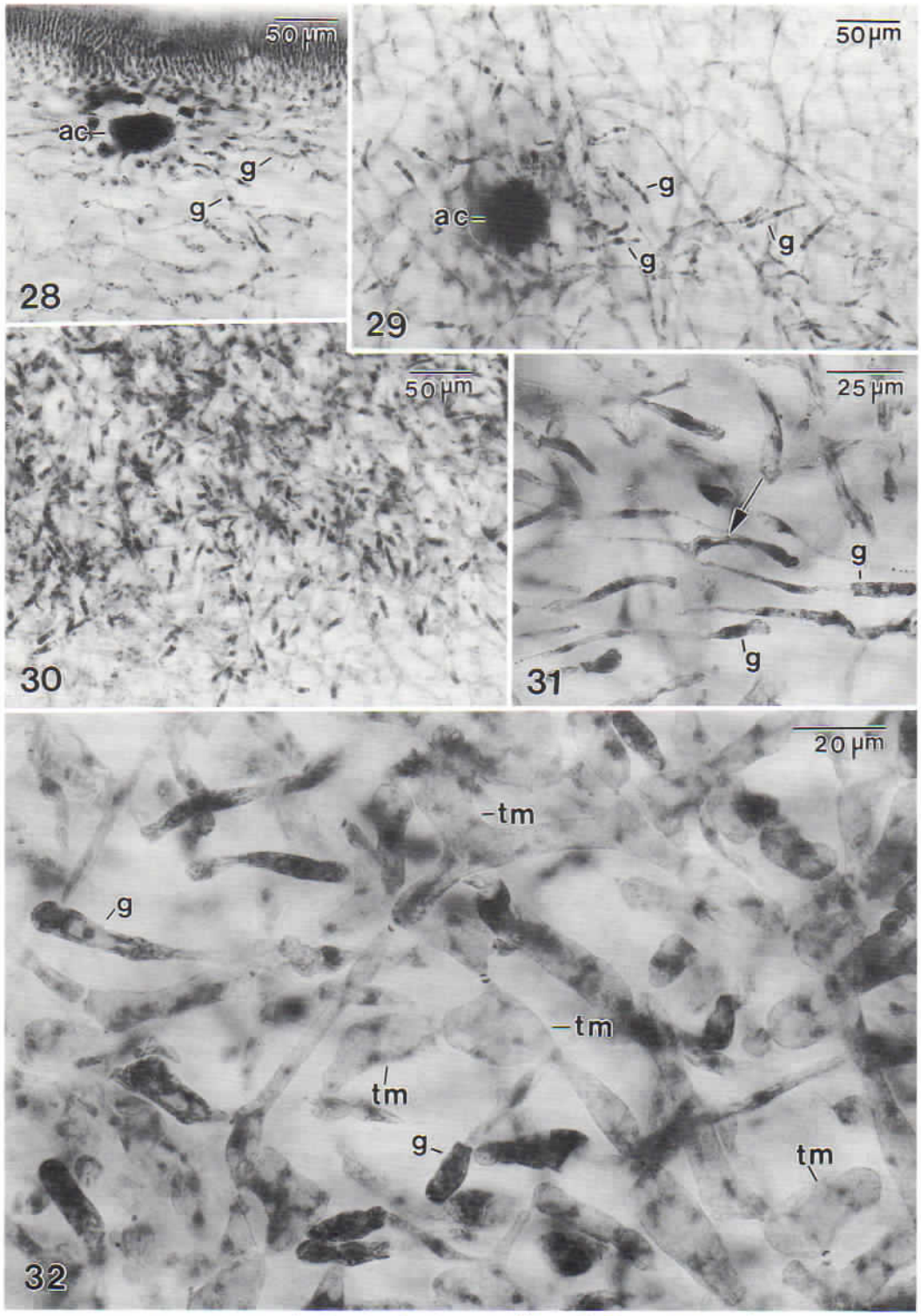
Fig. 17. Spermatangium (s) produced from terminal cortical cells at tip of gametophyte bearing cystocarps. Longitudinal section.
Fig. 18. Surface view showing procarp initials (pi) amongst outer cortical cells.
Fig. 19. Procarp initial (pi). Longitudinal section.
Fig. 20. Orientation of supporting cell (su), carpogonial branch initial (cbi) and initial of procarpial cortical filament (arrow) in relation to vegetative cortical filaments and surface cells. Oblique longitudinal section.
Fig. 21. Same stage as in Fig. 20. Longitudinal section.
Fig. 22. Supporting cell (su) bearing first cell of carpogonial branch (cb_1) with carpogonial initial (cbi) and initial of procarpial cortical filament (arrow). Longitudinal section.
Fig. 23. Supporting cell (su) bearing 3-celled carpogonial branch consisting of basal cell (cb_1), intercalary cell (cb_2), and carpogonium (cp) with terminal club-shaped trichogyne, and procarpial cortical filament (arrow). Longitudinal section.
Fig. 24. Auxiliary cell (ac) bearing enucleate protrusions (arrowheads). Note lack of envelope around auxiliary cell. Periclinal section.
Fig. 25. Auxiliary cell (ac) bearing remnant of carpogonial branch with trichogyne (t), enucleate protrusions and gonimoblast initials (arrowheads). Longitudinal section.
Fig. 26. Abortive multinucleate auxiliary cell (ac) showing darkly staining procarpial cortical filament (arrow), first two cells of carpogonial branch (cb), and enucleate, degenerating gonimoblast initials (arrowheads). Longitudinal section.
Fig. 27. Auxiliary cell (ac) bearing gonimoblast initials (arrowheads). Medullary cells immediately surrounding auxiliary cell have expanded in size and are darkly staining with many nuclei. Periclinal section.



Figs 28–32. *Chondrus crispus*. Post-fertilization development. Sidmouth, Devon, UK (*Brodie*, 5.v.1991, NCU).
Fig. 28. Auxiliary cell (ac) bearing filamentous gonimoblasts (g). Longitudinal section.
Fig. 29. Auxiliary cell (ac) bearing ramifying, filamentous gonimoblasts (g). Periclinal section.

many darkly staining nuclei, barely visible in Figs 24–26. Functional auxiliary cells form numerous enucleate protrusions from the cell surface. Ten to fifteen such protrusions may be seen in a single focal plane (Figs 24, 25). Auxiliary cells contain a mixture of large (10–13 μm) and small (4–5 μm) nuclei which are obscured owing to the density of the cytoplasm in our material. The enlarged nuclei that we observed in functional auxiliary cells contain amplified levels of DNA and correspond to the haploid vegetative nuclei that were originally present in the supporting cell prior to diploidization. Only the smaller, presumably diploid nuclei migrate into the enucleate protrusions and are cut off, one in each gonimoblast initial (Figs 25, 27). The carpogonial branch degenerates once the auxiliary cell has expanded, the cell contents disappear and a trichogyne remnant is sometimes seen extending through the thallus surface.

Procarps are often encountered that have evidently been fertilized but subsequently aborted. In such procarps, the multinucleate auxiliary cell, the sterile lateral filament, and the first two cells of the carpogonial branch often stain darkly (Fig. 26). Procarps are considered to have aborted if they fail to produce processes, or when all gonimoblast initials connected to the auxiliary cell have collapsed and their nuclei have degenerated (Fig. 26).

Only a few of the many gonimoblast initials emanating from an auxiliary cell elongate to produce septate, branched gonimoblast filaments (Fig. 28). The rest, including those directed towards the thallus surface, atrophy and ultimately disappear. Most gonimoblast filaments radiate laterally within the outer medulla, parallel to the thallus surface (Fig. 29); however, a few traverse the medulla and grow towards the opposite side (Fig. 28). Young gonimoblast filaments grow by means of uninucleate apical cells that are densely filled with cytoplasm at their tips and are narrow and highly vacuolate distally (Figs 29–32). Initially few in number (Fig. 29), gonimoblast filaments may become exceedingly abundant (Fig. 30). An apical gonimoblast cell may extend in length up to several times its diameter before dividing, the cytoplasm accumulates at the tip, and a new apical initial is cut off (Figs 31–32). Cytoplasm that concentrates at the apical end of a subterminal cell supports the production of a lateral branch (Fig. 31). Gonimoblast cells are about the same diameter as the narrowest secondary medullary cells (2–5 μm). They are distinguished by being uninucleate and tubular in shape, terminated by apical initials that are densely filled with cytoplasm.

Unmodified vegetative medullary cells are typically narrow with a central vacuole, and contain relatively few nuclei (Figs 27–29). A few medullary cells lying close to a functional auxiliary cell enlarge, become more densely filled with cytoplasm, and the number of nuclei increases (Fig. 27). Gonimoblast filaments are often seen ramifying amongst unmodified medullary cells or medullary cells that have been transformed (Figs 29–31). Transformation of the medullary cells, like the growth of the gonimoblast filaments themselves, progresses outwardly from the auxiliary cell. Figure 32 illustrates an area containing numerous gonimoblast filaments interwoven amongst the network of transformed medullary cells at a stage prior to linkage between the two tissues. A mixture of vegetative medullary cells, transformed medullary cells, and medullary cells undergoing transformation is apparent in Figs 33 and 34. Vegetative medullary cells are highly vacuolate with spindle-shaped nuclei. Transforming medullary cells enlarge, each of the nuclei divides simultaneously, and protein synthesis takes place accompanied by the disappearance of the central vacuole. In Fig. 33 the nuclei are all in metaphase with randomly oriented spindles in the cell undergoing transformation, and in Fig. 34 two gonimoblast filaments, one of which is in the process of branching, are observed approaching a medullary cell that is undergoing transformation with the nuclei all in anaphase. Only one synchronous nuclear division takes place in each cell, the number of nuclei doubles per cell, and the resulting cells are more densely filled with cytoplasm.

In the final stages of gonimoblast development, the gonimoblast filaments septate frequently in the vicinity of transformed medullary cells, producing short to moderately long, uni-

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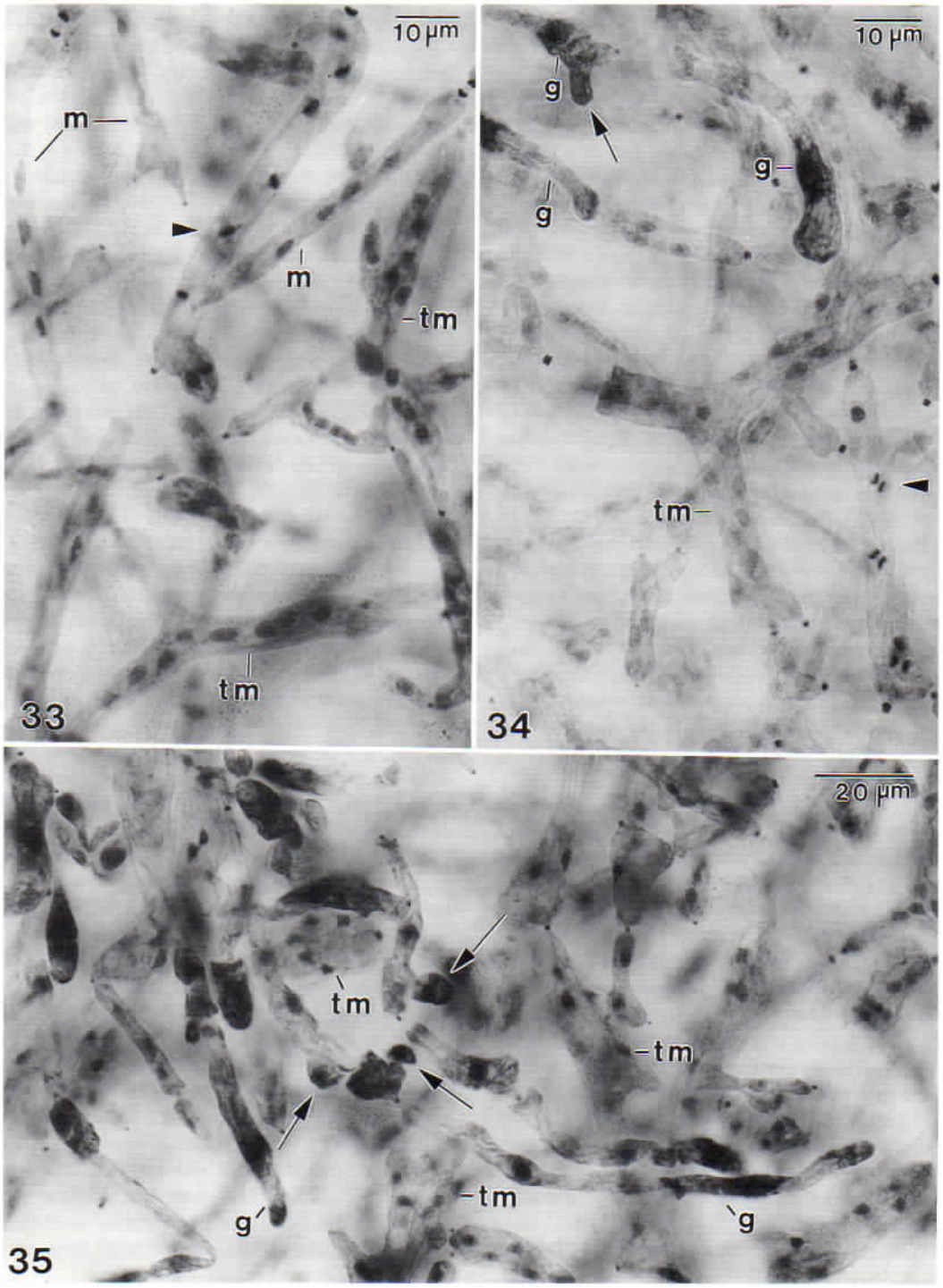
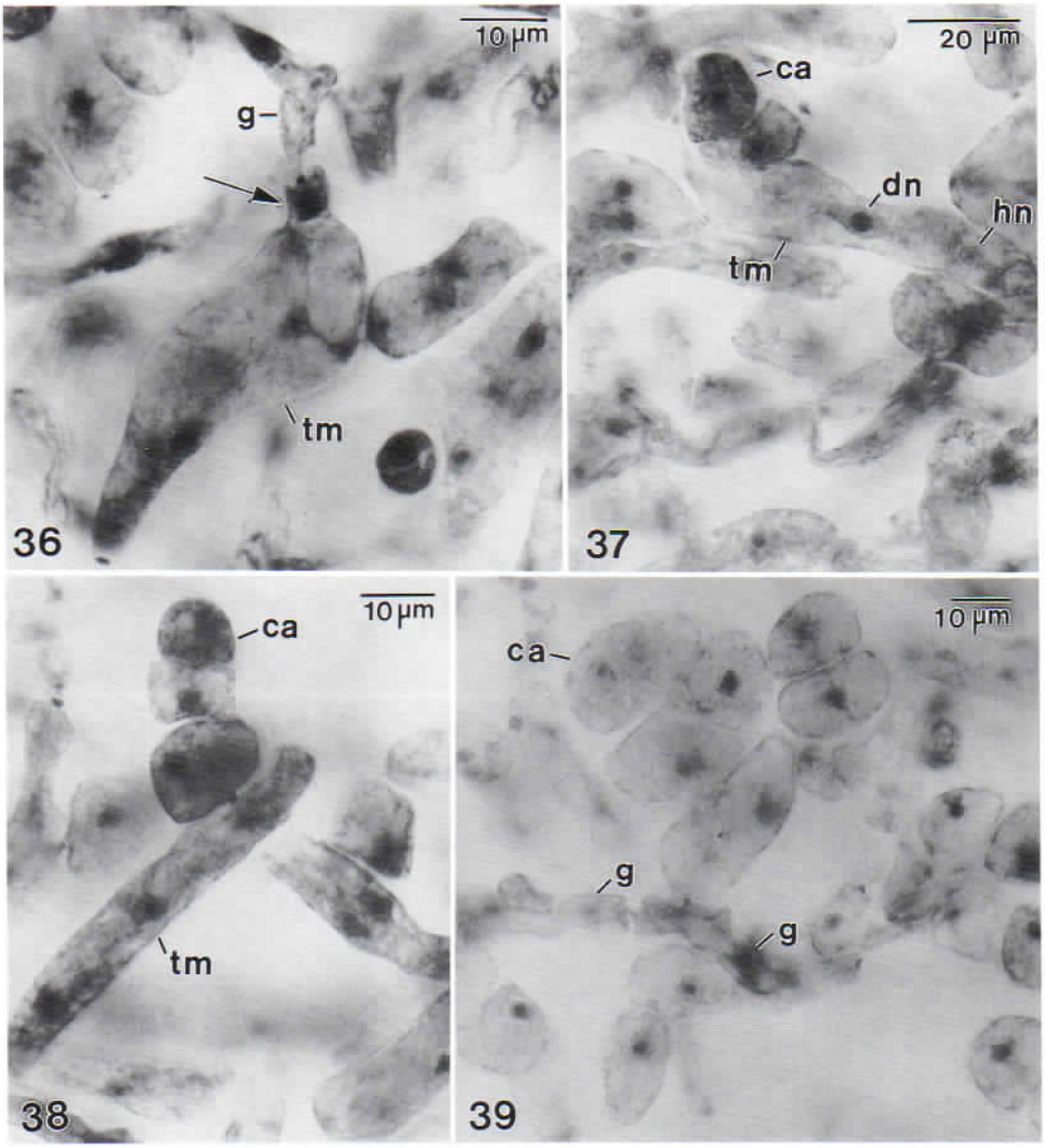
Fig. 30. Extensive mass of gonimoblast filaments ramifying at a distance from auxiliary cell. Periclinal section.
Fig. 31. Narrow, tubular, hyaline, gonimoblast filaments (g) with protoplasm-rich tips, initiating lateral branches (arrow). Periclinal section.
Fig. 32. Gonimoblast filaments (g) ramifying amongst enlarged, transformed medullary cells (tm). Periclinal section.



Figs 33–35. *Chondrus crispus*. Post-fertilization development in periclinal section. Sidmouth, Devon, UK (*Brodie*, 5.v.1991, NCU).

Fig. 33. Highly vacuolate medullary cell (m) containing spindle-shaped nuclei; medullary cell with nuclei undergoing simultaneous mitoses at metaphase stage with mitotic spindles (arrowhead); transformed medullary cell (tm) containing twice the previous number of nuclei in denser cytoplasm.



Figs 36–39. *Chondrus crispus.* Post-fertilization development in periclinal section. Sidmouth, Devon, UK (*Brodie*, 5.v.1991, NCU).

Fig. 36. Conjunctor cell (arrow) cut off from gonimoblast cell (g) fusing with transformed medullary cell (tm).

Fig. 37. Two-celled carposporangial chain (ca) cut off from transformed medullary cell (tm) containing a large, putatively diploid nucleus (dn) and small, haploid nuclei (hn).

Fig. 38. Three-celled carposporangial chain (ca) cut off from transformed medullary cell (tm).

Fig. 39. Carposporangial chain (ca) cut off from uninucleate gonimoblast cell (g).

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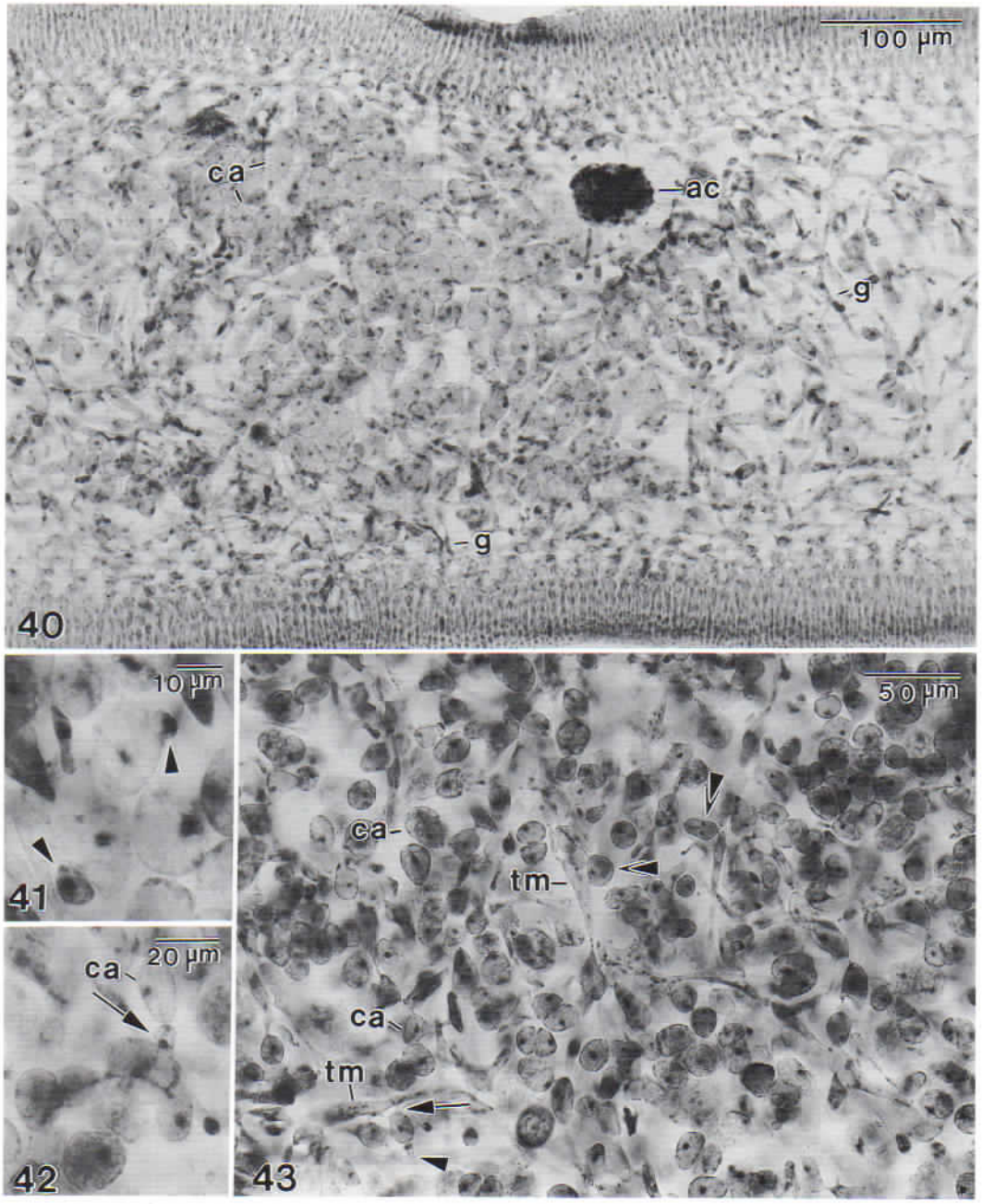
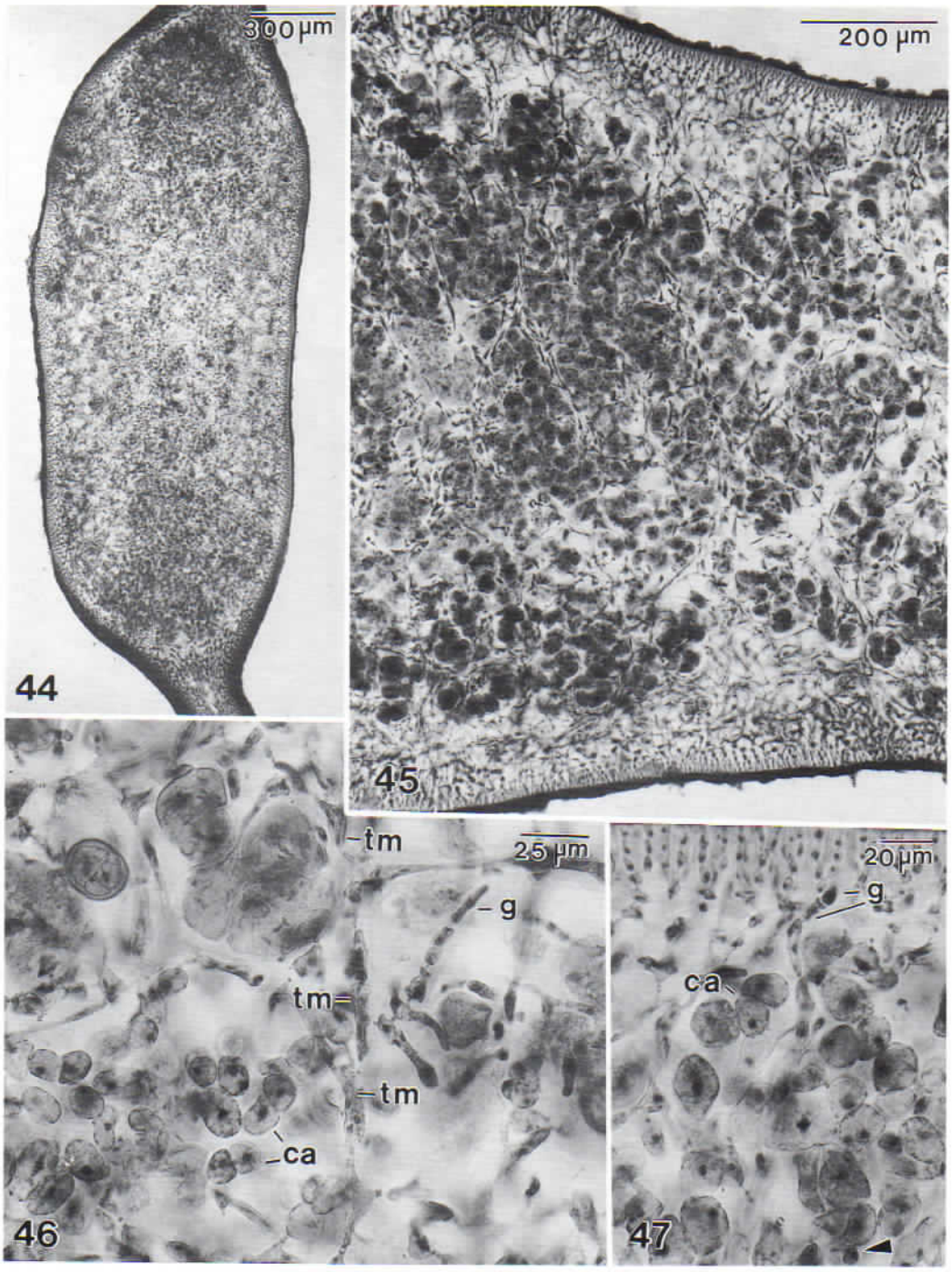
Fig. 34. Branching (arrow) gonimoblast filaments (g); medullary cell with nuclei undergoing simultaneous mitoses at anaphase stage (arrowhead); and transformed medullary cells (tm).

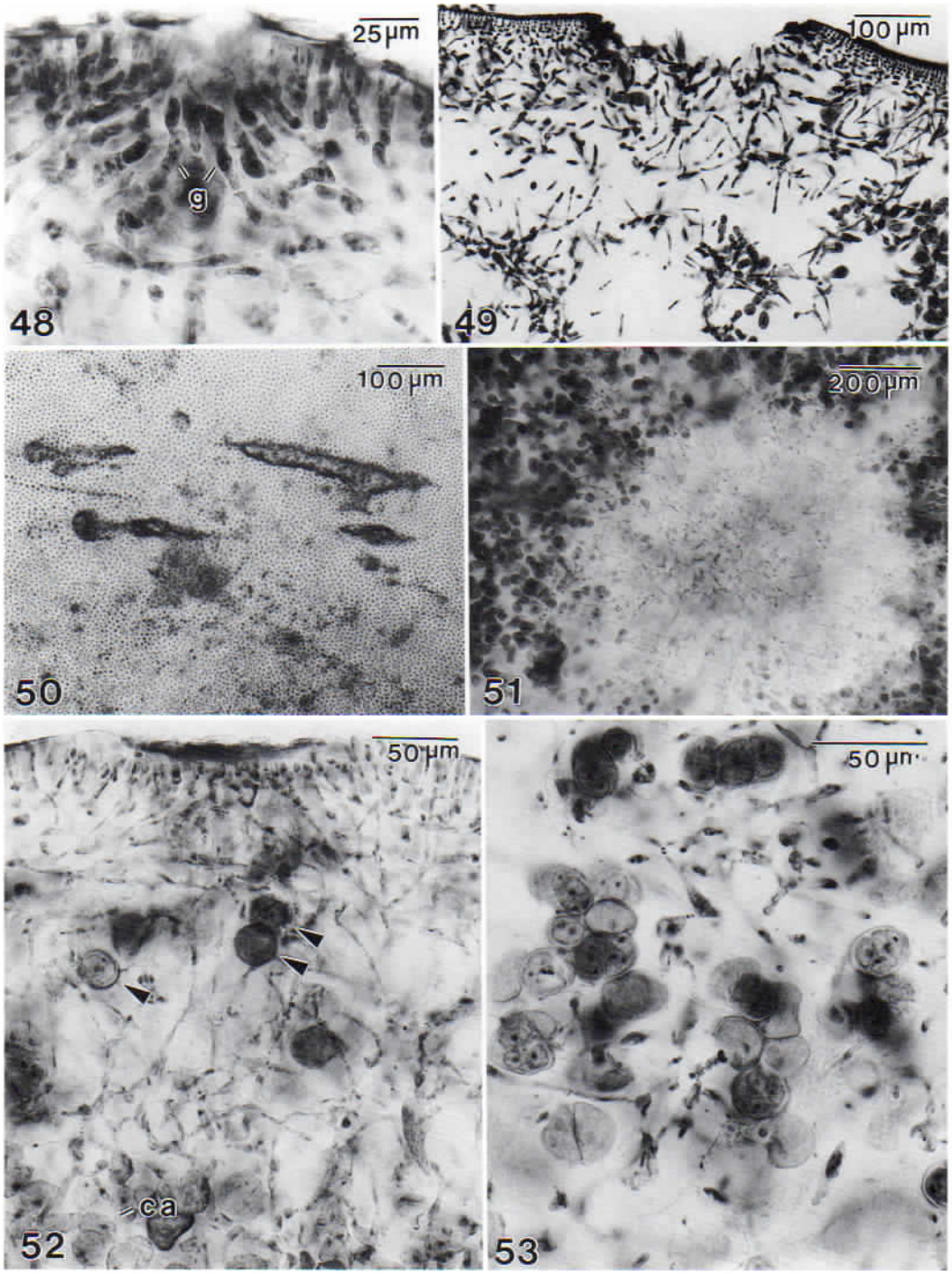
Fig. 35. Uninucleate gonimoblast filaments (g) with lateral conjunctor cells (arrows) ramifying amongst transformed medullary cells (tm).



Figs 40–43. *Chondrus crispus*. Post-fertilization development. Sidmouth, Devon, UK (*Brodie*, 5.v.1991, NCU).
Fig. 40. Cystocarp showing auxiliary cell (ac), carposporangia (ca) and gonimoblast filaments (g). (Note absence of secondary enveloping tissue.) Longitudinal section.
Fig. 41. Carposporangia cutting off conjunctor cells (arrowheads). Periclinal section.
Fig. 42. Conjunctor cell cut off from one carposporangium (ca) fusing (arrow) with a neighbouring carposporangium. Periclinal section.
Fig. 43. Stretched network of transformed medullary cells (tm) bearing carposporangial chains (ca) intermixed with multinucleate cells modified from potential carposporangia (double arrowheads). Carposporangia cut off conjunctor cells (arrowhead) forming secondary pit connections (arrow) upon fusion with neighbouring cell. Periclinal section.



Figs 44–47. *Chondrus crispus.* Mature cystocarps. Sidmouth, Devon, UK (*Brodie,* 5.v.1991, NCU).
Fig. 44. Mature cystocarp. Transverse section.
Fig. 45. Mature cystocarp containing carposporangia and darkly staining secondary gonimoblast filaments that grow amongst the carposporangia and reach the outer cortex. Transverse section.
Fig. 46. Branched gonimoblast filaments (g) formed secondarily from transformed medullary cells (tm) in network which also bear carposporangia (ca). Periclinal section.
Fig. 47. Secondary gonimoblast filaments (g) penetrating outer cortex. Carposporangia (ca) continue cutting off conjunctor cells (arrowhead). Longitudinal section.



Figs 48–53. *Chondrus crispus.* Mature cystocarp. Sidmouth, Devon, UK (*Brodie*, 5.v.1991, NCU).
Fig. 48. Second gonimoblast filaments (g) pushing aside surface cortical filaments causing gap in cuticle. Longitudinal section.
Fig. 49. Expanded secondary gonimoblast filaments filling space below gap in cuticle. Longitudinal section.
Fig. 50. Multiple surface fissures in outer cuticle through which carpospores are released. Surface view.
Fig. 51. Optical section below a fissure showing central area of cystocarp with empty filamentous network, and carposporangia at periphery.

nucleate segments that contain varying amounts of cytoplasm. Such intercalary gonimoblast cells cut off conjunctor cells that grow towards the transformed medullary cells (Fig. 35) and fuse with them, depositing their supposedly diploid nucleus (Fig. 36). The result is a heterokaryotic cell that appears to contain both haploid and diploid nuclei. Putative diploid nuclei are about twice the diameter (5–7 μm) of supposedly haploid nuclei (2–2.5 μm) and contain a single, prominent nucleolus (Fig. 37). Both heterokaryotic medullary cells (Figs 37–38) and unfused, intercalary gonimoblast cells (Fig. 39) can produce short chains of carposporangia up to 4–5 cells long; however, the majority of carposporangial chains originate from the transformed medullary cells. A potential carposporangium contains a single diploid nucleus 4–5 μm in diameter.

Vegetative medullary cells produce few or no secondary filaments and an enveloping tissue is absent. Once the gonimoblast filaments have cut off conjunctor cells, the formation of carposporangial chains follows soon after, and the gonimoblasts reach an outer limit that apparently establishes the boundary of the mature cystocarp.

Carposporangia of different ages can be seen in the same cystocarp, as they do not mature simultaneously (Figs 40, 44, 45, 46). Potential carposporangia frequently cut off conjunctor cells (Figs 41–42) that fuse either with neighbouring carposporangia or with transformed medullary cells. A cell that receives a second nucleus is converted into a vegetative cell and becomes part of the supporting network (Figs 42–43). Only uninucleate cells mature into carposporangia. The mature cystocarp thus consists of medullary cells, remnants of the primary gonimoblasts, branched carposporangial chains linked to transformed medullary cells, and dedifferentiated carposporangia that have been incorporated secondarily into the filamentous network (Fig. 43). It bulges on one or both sides of the thallus bounded by the original cortex (Fig. 44).

In addition to the carposporangia and transformed medullary cells, the cystocarp becomes filled with darkly staining filaments, most of which issue from transformed, heterokaryotic medullary cells. Such adventitious gonimoblast filaments are composed of short, uninucleate cells containing only putatively diploid nuclei. The gonimoblast filaments branch irregularly, grow through the surrounding medullary tissues (Figs 45, 46), penetrate between the cortical filaments (Fig. 47), and disrupt the cuticle (Fig. 48). Multiple gaps develop in the outer layer (Figs 49, 50) through which the carpospores are released. The central area below a group of such gaps is commonly devoid of carposporangia (Figs 49–51), while carposporangia are still intact at the periphery (Fig. 51). An empty halo-like central area can be easily mistaken for an ostiole by the unaided eye.

Carposporangia are sometimes retained within the emptied cystocarp (Fig. 52) and germinate *in situ* (Fig. 53). Secondary cortical filaments proliferate beneath a gap and a new cuticle is formed, repairing the damaged area. Additional secondary gonimoblast filaments fill the central area as the process of tissue repair continues (Fig. 52). The release of carpospores may leave holes in the thallus, but most of the damaged tissue is usually repaired.

TETRASPORANGIAL REPRODUCTION: Tetrasporangial sori are initiated entirely within the medulla. Short chains of tetrasporocytes are produced secondarily from primary medullary cells (Figs 54, 56), and initially consist of short chains, 3–4 cells long which are not terminally pit-connected (Fig. 55). Most tetrasporocyte chains grow transversely and link to medullary cells in separate cell lineages by means of secondary pit connections (Figs 55, 56). Tetrasporocytes divide successively into four cruciately arranged tetraspores to give tetrasporangia that are 40–45 μm long and 30–35 μm broad (Fig. 57). The expanded medullary cells, which are initially stellate in shape (Fig. 56), collapse as their contents are depleted during maturation of the tetrasporangia (Fig. 57). At maturity, tetrasporangia fill the entire medulla (Fig. 58). The cortex is not involved in the formation of tetrasporangia.

Circular pores form in the cuticle on both surfaces of a tetrasporangial sorus (Figs 59, 60). Gelatinous material accumulates around the mouth of the pores, suggesting that the mechanism of tetraspore release involves gelatinous extrusion (Fig. 60). Secondary cortical filaments proliferate

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Fig. 52. Old sorus after most of the carpospores have been released. Some retained carpospores encyst *in situ* (arrowheads). Longitudinal section.

Fig. 53. Germinating carpospores inside cystocarp. Longitudinal section.

within the subcortex in the region of a pore and a new cuticle is formed, repairing the damaged area (Fig. 61).

DISCUSSION

Vegetative development

The growing apices of juvenile uprights and adult thalli of *Chondrus crispus* are very similar anatomically, the principal difference being that the meristem is dome-shaped in the former and is extended across the apex in the plane of flattening in the latter. As in *Gigartina pistillata* (S.G. Gmelin) Stackhouse (Hommersand *et al.* 1992), the meristem extends only a short distance (0.5 mm to 1.0 mm) behind the tip, and cell division and cell expansion virtually cease further below. Primary meristematic activity does not appear to extend a great distance along the margin in *C. crispus* as, for example, in *Gigartina exasperata* Harvey et Bailey, nor is it diffuse over the thallus surface, as in *Iridaea cordata* sensu Abbott (1971) [non *Iridaea cordata* (Turner) Bory] (Norris & Kim 1972).

The apex of *Chondrus crispus* exhibits fountain-type growth, as was illustrated by Darbishire (1902, fig. 6) and Kylin (1923, fig. 10a), with the formation of a primary network in which virtually every cell is connected to each of its neighbouring cells, either by a primary or a secondary pit connection. The network is more or less regular owing to the fact that nearly every apical cell divides longitudinally and branches pseudodichotomously. Alternating transverse and longitudinal apical cell divisions, such as occur in *Gigartina pistillata* (Hommersand *et al.* 1992), are rare in *C. crispus* and vegetative intercalary cell divisions appear to be absent. The cortex is constant in thickness at approximately 6–7 cell layers, and medullary cells expand laterally in the plane of flattening. Secondary filaments are narrow, rarely more than one cell long, and connect to cells below by means of terminal conjunctor cells forming secondary pit connections. As was the case with secondary pit connections, secondary filaments seldom, if ever, link to cells in the same cell row. Like many members of the Gigartinaceae, and unlike *G. pistillata* (Hommersand *et al.* 1992), primary and secondary vegetative medullary cells do not distend or become inflated, but retain their original shape or become stretched, and the intercellular space created by thallus expansion is filled by the production of additional one-celled secondary filaments. Dichotomous branching takes place in *C. crispus* when a portion of the apical meristem ceases to grow, as indicated by the failure of intercalary cells to produce lateral conjunctor cells and secondary pit connections. This is different from dichotomous branching in *G. pistillata* (Hommersand *et al.* 1992) in which the apical initials and their derivative filaments separate into two masses, establishing two new apices at the time of branching.

Of the species of *Chondrus* reported from the eastern North Pacific, the morphology and vegetative anatomy of *C. crispus* most closely resembles that of *C. nipponicus* (Brodie *et al.* 1991). This species, which was formerly treated as *Chondrus crispus* by Japanese investigators (see Mikami 1965), is not so regularly dichotomously branched and often bears lateral proliferations. The medullary filaments of *C. nipponicus* are generally shorter and less densely packed than those of *C. crispus* (Brodie *et al.* 1991).

Reproductive development

Spermatangia arise singly or in pairs from superficial cortical cells in *Chondrus*, as was pre-

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Figs 54–61. *Chondrus crispus*. Tetrasporangial sorus. Spanish Point, County Clare, Ireland (*Hommersand*, 2.vii.1985, NCU).

Fig. 54. Sorus containing chains of tetrasporocytes (t) inside the medulla. Longitudinal section.

Fig. 55. Three-celled chain of tetrasporocytes (t) cut off from medullary cell (m), and tetrasporocytes linking to medullary cells by secondary pit connections (arrows). Longitudinal section.

Fig. 56. Network of elongated medullary cells (m) bearing chains of tetrasporocytes (t) many of which become intercalary, having linked to other medullary cells (arrow). Periclinal section.

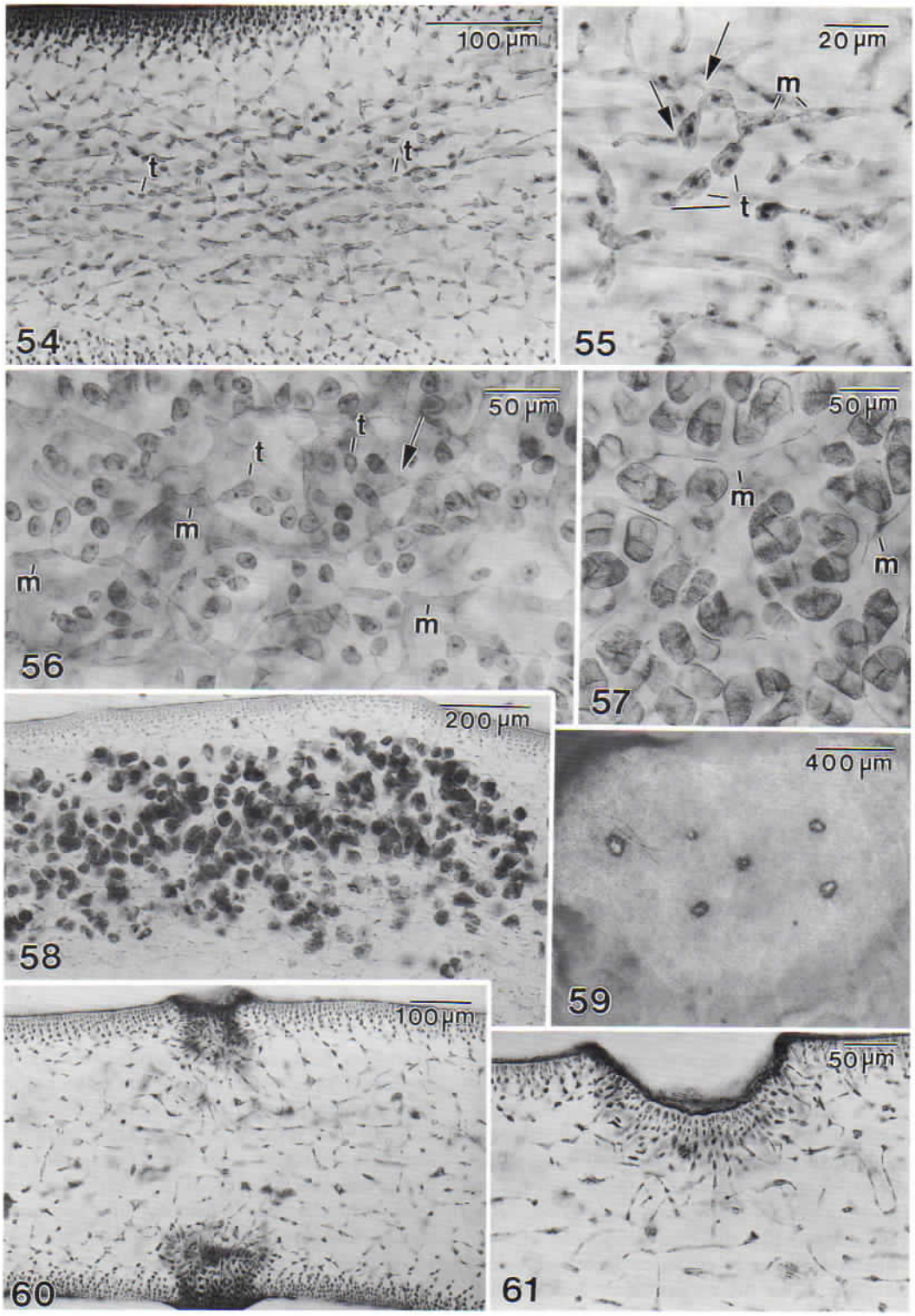
Fig. 57. Cruciately divided tetrasporangia amongst collapsed medullary cells (m). Periclinal section.

Fig. 58. Mature tetrasporangial sorus. Longitudinal section.

Fig. 59. Tetrasporangial sorus with multiple surface pores. Surface view.

Fig. 60. Longitudinal section through margin of two opposite pores with condensed gelatinous matrix. Subcortical cells surrounding pores have generated secondary filaments.

Fig. 61. Centre of a former pore repaired by secondary cortex and with a new outer cuticle. Longitudinal section.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viously described by Darbishire (1902, fig. 32), Prince & Kingsbury (1973), Tazawa (1975), and Brodie *et al.* (1991). The site of procarp development is linked directly to the mode of vegetative growth in *C. crispus*. Procarps are formed across the thallus surface within 1 mm of the apex and are visible for a centimetre or more behind the tips, even though they may no longer be functional. The procarp initial is a surface cell and the curved, 3-celled carpogonial branch is formed from the apical cell of the leading cortical filament, while a subterminal lateral initial produces a vegetative cortical filament, as in *Gigartina pistillata* (Hommersand *et al.* 1992). A reexamination of the procarp of *Chondrus nipponicus* (Brodie *et al.* 1991) showed that a sterile lateral filament is also present in the procarp of that species. The carpogonium is reported to fuse directly with the supporting cell in *C. crispus* (Kylin 1923; Prince & Kingsbury 1973), which functions as an auxiliary cell.

Functional auxiliary cells enlarge symmetrically, contain a mixture of large and small nuclei, and produce large numbers of enucleate protrusions from the surface in *C. crispus*, as in most members of the Gigartinaceae. As was the case in *G. pistillata* (Hommersand *et al.* 1992), only the small, presumably diploid nuclei migrate into the enucleate protrusions and are cut off upon formation of the gonimoblast initials. Though many of the details were previously unclear, this stage has been illustrated many times in various members of the Gigartinaceae, including *C. crispus* (Kim 1976) and species of *Chondrus* from Japan (Mikami 1965: Brodie *et al.* 1991). The gonimoblast filaments of *Chondrus* are exceedingly fine, as narrow as any recorded in the phyllophoracean genus *Gymnogongrus* (Mikami 1965), and narrower than those seen in other genera of the Gigartinaceae. They exhibit a type of apical growth usually associated with the most delicate connecting filaments found in non-procarpic members of the Gigartinales (Hommersand & Fredericq 1990), in which existing cytoplasm is concentrated at the tips, and new cell contents are synthesized before cell division in successive apical cells and subterminal cells at branching points. Intercalary gonimoblast cells of *C. crispus*, like the intercalary cells of true connecting filaments, are uninucleate and highly vacuolate. Even the narrowest medullary cells are usually multinucleate and linked to one another to form the medullary network.

Mikami (1965) repeatedly states that the gonimoblast threads elongate and communicate with swollen medullary cells in the vicinity of the auxiliary cell in the course of cystocarp development in Japanese species of *Chondrus*. His illustrations of *C. nipponicus* (as *C. crispus*), in particular, show short, broad modified medullary cells being contacted by gonimoblast cells. Brodie *et al.* (1991, fig. 39) illustrate developing carposporangia linked to swollen, multinucleate vegetative cells in *C. nipponicus*, and Kim (1976, fig. 148) has depicted enlarged medullary cells contacted by gonimoblast filaments in the vicinity of an auxiliary cell. Thus, it appears that medullary cells normally swell around functional auxiliary cells and in the vicinity of gonimoblast filaments in all species of *Chondrus*. Intercalary divisions are rare or absent in most species of *Chondrus*, with the possible exception of *Chondrus elatus* Holmes (Mikami 1965). There are no reports, so far, of the production of secondary filaments by medullary cells inside a developing cystocarp. Indeed, the absence of an enveloping tissue, or any other type of secondary gametophytic filaments, was a key diagnostic character used by J. Agardh (1851, 1876) in separating *Chondrus* from all other genera belonging to the Gigartinaceae, and has been recognized by all investigators since (Kylin 1923; Mikami 1965; Kim 1976).

Medullary cells expand, increasing the thickness of the cystocarp, and gonimoblast filaments grow between the medullary cells and cut off conjunctor cells that fuse onto the modified medullary cells, forming secondary pit connections in *C. crispus*. Similarly, conjunctor cells and secondary pit connections linking gonimoblast filaments to medullary cells were seen and illustrated by Mikami (1965, figs 23–25) in most Japanese species of *Chondrus*. Such linkages may function solely for the support or nutrition of the gonimoblasts by the medulla or, as in *C. crispus*, apparently diploid nuclei may divide inside the medullary cells, and they, in turn, function as generative cells for the production of carposporangial chains. Since developing carposporangia may, themselves, cut off conjunctor cells that fuse with medullary cells, care must be taken in every instance to distinguish clearly between medullary cells that are forming carposporangial chains, and carposporangia that may be linked secondarily to medullary cells. Mikami's (1965, figs 10, 25) elegant illustrations of Japanese species of *Gymnogongrus* and *Chondrus* all show carposporangial chains emanating from gonimoblast filaments and not from medullary cells.

The same is true of Kylin's (1923, fig. 11c) illustration for *Chondrus crispus*. Kim (1976, p. 32) questioned whether carposporangial mother cells are always derived from gonimoblast filaments in *C. crispus*, and suggested that the enlarged female cells around the gonimoblast filaments may 'transform to carposporangial mother cells'. Our studies of *C. crispus* show that, while some carposporangial chains are produced by gonimoblasts, the majority derive from transformed medullary cells that have received putative diploid nuclei after fusion with conjunctor cells cut off from gonimoblasts. In this respect they are like *Gigartina pistillata*, the only other member of the Gigartinaceae in which it has been shown that carposporangial chains are derived both from gonimoblast cells and from vegetative cells contacted by gonimoblasts (Hommersand *et al.* 1992). In this latter instance, however, most of the gametophytic cells producing carposporangial chains are not medullary cells but, instead, are cells of the enveloping tissue and, hence, of secondary origin. In our experience, gametophytic cells that function solely in the support and nutrition of the gonimoblasts soon collapse after linkage has been established, whereas the generative gametophytic cells of *C. crispus* and *G. pistillata* remain turgid longer. It remains to be established whether the medullary cells of Japanese species of *Chondrus* are entirely nutritive, or if they are able to generate carposporangial chains in the manner we have described here in *C. crispus*.

The behaviour of the gonimoblast filaments in *Chondrus* is interesting in light of the hypothesis by Drew (1954) that connecting filaments found in non-procarpic red algal families evolved from gonimoblast filaments. Drew distinguished between 'primary gonimoblasts', that initially distribute the fertilization nucleus, and 'secondary gonimoblasts' that produce the carposporangia. She also 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 produced the 'secondary gonimoblasts'. While it is doubtful that anyone would call the gonimoblasts of *Chondrus* 'connecting filaments', or the medullary cells 'auxiliary cells', they do share certain structural and functional similarities, and the medullary cells act either as nutritive or as generative cells in the production of the carposporangial chains. Drew (1954, p. 65) was careful to state that true auxiliary cells are 'specified', which is not true of the medullary cells that bear the carposporangia in *C. crispus*. Nevertheless, the gonimoblasts and medullary cells in this species illustrate one way in which connecting filaments and auxiliary cell systems could have evolved.

We saw approximately ten examples in which medullary cells in the vicinity of gonimoblast filaments were undergoing mitosis, two of which are illustrated in this paper (Figs 33, 34). In every instance, the nuclei were all in exactly the same stage of either metaphase or anaphase, and nuclear division was always followed by protein synthesis, resulting in more darkly staining cells containing twice the previous number of nuclei. Since the growth of the gonimoblast filaments and the transformation of medullary cells were never completely synchronous, we assume that gonimoblast formation and the transformation of the medullary cells are separate, though related processes. The most likely explanation is that a functional auxiliary cell radiates a hormonal signal which triggers dedifferentiation and transformation of the medullary cells, in addition to producing the gonimoblasts. Supposedly diploid nuclei enter the transformed medullary cells in *C. crispus*, divide, and are the source of nuclei employed in generating the carposporangial chains. Since carposporangial chains derive predominantly from transformed medullary cells, with the rest coming from gonimoblast cells, the developmental process is neither singular nor entirely fixed.

Not all primary or secondary gonimoblast filaments mature into carposporangial chains; many traverse the medulla and enter the cortex, swelling the cystocarp and initiating gaps in the outer cuticle through which the carpospores are released. Additional gonimoblast filaments produce secondary carposporangial chains, extending the life of the cystocarp. It would not be surprising if phenological studies showed that an individual cystocarp remains reproductive throughout an entire growing season. The holes one sees towards the base in some old female thalli may represent the remains of cystocarps generated during the previous season. Moreover, carpospores that remain and germinate *in vivo* may be released during the final rupture of an old cystocarp.

Tetrasporangial sori fill the centre of the medulla and the tetrasporangial chains consist of short filaments that bridge between files of medullary cells and link to cells in separate filaments

by means of secondary pit connections. Mikami (1965) has illustrated a similar behavior in *C. pinnulatus* (Harvey) Okamura, *C. giganteus* Yendo, and *C. nipponicus* (as *C. crispus*) from Japan. In other Japanese species, the tetrasporangial sori originate from either side of the medulla, near the boundary between inner cortex and medulla and extend inwardly, as in *C. ocellatus* Holmes, *C. yendoi* Yamada et Mikami, and *C. verrucosus* Mikami. Tetraspore release is effected by gelatinous extrusion through multiple circular pores in the outer cuticular layer, and does not resemble carpospore release from cystocarps. Tissue repair is brought about by the formation of secondary vegetative filaments, as opposed to repair by the further growth of gonimoblast filaments in cystocarps. All tetrasporangia are derived from secondary filaments in *Chondrus*, in contrast to the condition in *Gigartina pistillata* (Hommersand *et al.* 1992) and many other Gigartinaceae, in which at least some tetrasporangia are transformed from cells in primary filaments.

CONCLUSIONS

The studies of *Chondrus crispus* reported here, and those of Mikami (1965) on species of *Chondrus* from Japan, support the original proposal by J. Agardh (1851, 1876) that *Chondrus* is separable from all other genera placed in the Gigartinaceae on the basis that the 'nucleus' of the cystocarp extends indefinitely through the surrounding vegetative tissue, unrestrained by any bounding filamentous network. Specifically, the gonimoblast filaments ramify through the network of swollen medullary cells and link to them by means of secondary pit connections. No additional secondary medullary or enveloping filaments are produced. *Chondrus canaliculatus* (C. Agardh) Greville from Pacific South America, which possesses an enveloping tissue, is different from typical *Chondrus* (Kim 1976). Tetrasporangia are all produced in secondary filaments in *Chondrus*, none being transformed from primary cortical or medullary cells. Even though some details of cystocarp development require reinvestigation, it is clear that most, if not all, of the species treated by Mikami (1965) belong in *Chondrus* as defined here. It may well be that carposporangial chains are partly derived from medullary cells only in *C. crispus* from the North Atlantic Ocean. If so, the North Atlantic and North Pacific species have probably been geographically isolated for a long time, probably longer than the period since the opening of the Bering Strait at *c.* 3.5 Ma. The North Pacific and North Atlantic assemblages should, nonetheless, be kept together in *Chondrus*, barring new evidence to the contrary. Long-standing records of *Chondrus crispus* from the Bering Sea, Aleutian Islands and Alaska (Lindstrom 1977) require reinvestigation.

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