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THE MORPHOLOGY OF *AGARDHIELLA SUBULATA* REPRESENTING THE
AGARDHIELLEAE, A NEW TRIBE IN THE SOLIERIACEAE
(GIGARTINALES, RHODOPHYTA)¹

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ABSTRACT

Agardhiella subulata (C. Agardh) Kraft et Wynne is a commonly collected erect, terete, alternately branched, fleshy red alga that is found both intertidally and subtidally in the western Atlantic Ocean, Caribbean Sea and Gulf of Mexico. A single periaxial cell is cut off from each succeeding axial cell in an orthostichous file. The supporting cells of carpogonial branches are homologous with auxiliary cells, being transformed from identical inner cortical cells. The auxiliary cell together with the three to four enlarged, darkly-staining cortical cells pit-connected to it form the auxiliary cell complex. Following fusion of a connecting filament to an auxiliary cell the diploid nucleus divides with one nucleus remaining near the point of fusion and the other migrating to the beaked portion of the auxiliary cell. Surrounding vegetative cells divide, forming files of cells that grow toward the auxiliary cell to form the involucre. Cells of the gonimoblast fuse with nearby cortical cells producing a placenta of vegetative and gonimoblast tissue. As the cystocarp matures the inner placental cells become vacuolate while at the periphery terminal and short, unbranched files of gonimoblast cells mature into carposporangia. Tetrasporangia are cut off laterally from surface cells and undergo basal elongation followed by lateral expansion before dividing zonately. *A. subulata* exhibits a combination of distinctive vegetative and reproductive features when compared with *Solieria* and thus serves as the type of a new tribe, the *Agardhielleae*, in the family *Solieriaceae*.

Key index words: *Agardhiella subulata*; *Agardhielleae*; *Gigartinales*; *Solieriaceae*

Agardhiella subulata (C. Agardh) Kraft et Wynne (1979) is a conspicuous member of the intertidal flora in Atlantic North America from Cape Cod, Massachusetts, to Indian River, Florida. The actual distribution of this species both to the north and south of its central range is clouded owing to nomenclatural and taxonomic difficulties as well as misidentifications. In recent times this taxon has gone under the names *Agardhiella tenera* (J. Agardh) Schmitz (Taylor 1937, 1960), *Agardhiella baileyi* (Harvey ex Kützing) Taylor (in Taylor and Rhyne 1970), and *Neoagardhiella baileyi* (Harvey ex Kützing) Wynne et Taylor (1973). The most recent combi-

nation, *Agardhiella subulata* (C. Agardh) Kraft et Wynne, is owing to the discovery of an older basionym applicable to this species, *Sphaerococcus subulatus* C. Agardh (1822).

Agardhiella subulata is one of the most thoroughly studied members of the *Solieriaceae* with many details of its vegetative and reproductive development described and illustrated by Harvey (1853, as *Solieria chordalis*), Osterhout (1896, as *Rhabdonia tenera*), Kylin (1928, as *Agardhiella tenera*), Taylor and Rhyne (1970, as *Agardhiella baileyi*), and Wynne and Taylor (1973, as *Neoagardhiella baileyi*). However, conflicting interpretations about its vegetative and reproductive development and the lack of information about critical developmental stages in cystocarp formation warrant further investigation. Moreover, detailed morphological information is required to clarify problems arising from nomenclatural changes and uncertain records of distribution. This paper reinvestigates the developmental morphology of *A. subulata* and attempts to resolve some of the outstanding taxonomic and phylogeographic problems.

MATERIALS AND METHODS

Our study is based on an investigation of material of *Agardhiella subulata* preserved in 5% formalin in seawater and collected from sites between Woods Hole, Massachusetts and Key West, Florida. Gabrielson (1980) gives a complete list of the *A. subulata* specimens examined.

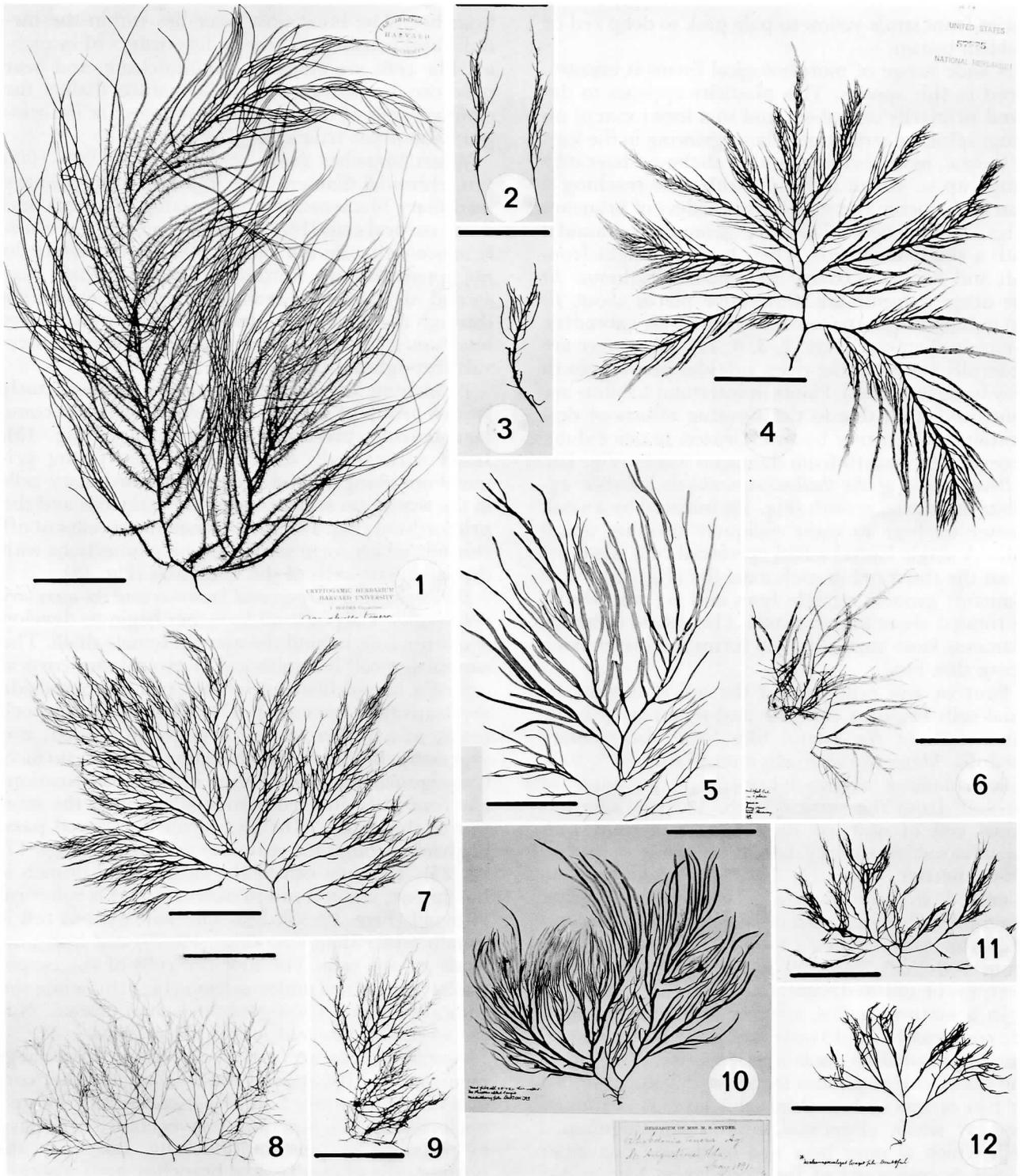
Material was sectioned by hand or on the freezing microtome at 40 μ m. Sections were stained in 1% aniline blue and 0.5% HCl until the appropriate stain density was achieved. Sections were washed in seawater and mounted in a 95:1:1 mixture of 20% corn syrup, 1% aniline blue and 0.5% HCl. Nuclei were stained using the aceto-iron-haematoxylin-chloral hydrate method of Wittmann (1965). Photographs and drawings are of aniline blue stained material unless otherwise noted. Drawings were made with the aid of a camera lucida; photographs were taken on a Zeiss Photomicroscope III.

RESULTS

Habit. Plants of *Agardhiella subulata* grow erect from a single attachment disc and bear few to many terete branches which commonly taper at their point of attachment to an axis (Figs. 2, 3, 7, 8). Branching is commonly alternate, although subopposite branching and branching in one plane also occur (Figs. 4, 5). Apices of branches range from truncate (Figs. 5, 10) to long attenuate (Fig. 1). Colorless deciduous hairs are present on the branches of young plants, but absent on old plants. The color of thalli

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FIGS. 1-12. Habits of *Agardhiella subulata* illustrating the range of variation in the species. Scales = 7 cm. Letters in parentheses indicate herbaria where specimens are housed. FIG. 1. Bridgeport, Conn. Robust tetrasporophyte covered with short proliferations due to in-situ germination of tetrasporangia (F). FIG. 2. Bogue Sound, N.C. (NCU). FIG. 3. As in Fig. 2, cystocarpic (NCU). FIG. 4. Burton's Bay, Va., cystocarpic (US57575). FIG. 5. Radio Island Jetty, Beaufort, N.C. (NCU). FIG. 6. In 25.5 m off Cubagua Island, Venezuela, cystocarpic (MICH). FIG. 7. Miami, Fla., tetrasporic (F). FIG. 8. Woods Hole, Mass. (NCU). FIG. 9. Børgesen specimen from Christiansted, St. Croix, cystocarpic (MICH). FIG. 10. St. Augustine, Fla. (MICH). FIG. 11. Radio Island Jetty, Beaufort, N.C., cystocarpic (NCU). FIG. 12. Bahia Matanzas, Cuba (MICH).

varies from straw-yellow to pale pink to deep red or reddish-brown.

A wide range of morphological forms is encountered in this species. This plasticity appears to depend primarily on habitat and to a lesser extent on geographical distribution. Plants growing in the lower littoral, in tidal creeks, and in sheltered bays may range up to 40 cm in height with axes reaching 4 mm in diameter and may have 4 orders of branches (Figs. 1, 7). These plants are generally pyramidal with a single main axis. Their texture ranges from soft and flaccid to coarse and sub-cartilaginous. At the other extreme are diminutive plants about 10 cm in height with narrow branches rarely exceeding 2 mm in diameter (Figs. 2, 3, 8, 11). The latter are generally found in the deep subtidal where growth may be light-limited. Plants in intertidal habitats are short and stout due to the stunting effects of desiccation and grazing by fish. Grazed plants exhibit regenerated growth from damaged apices (Fig. 10).

Development of the thallus. *Agardhiella subulata* exhibits multiaxial growth (Fig. 13) initiated by a small cluster of four to eight obliquely dividing apical cells. A single lateral initial (periaxial cell) is cut off from the third cell in each axial file (Fig. 25). Axial filaments grow in straight lines and are not twisted or rotated about a central axis. The system of lateral filaments from each axial cell forms the cortex lying above that file.

Four or five cells behind the apical initials the axial cells begin to elongate and together with the inner cells of the lateral files form the primary medulla. Many of these cells cut off a single 2- to 3-celled filament oriented laterally at an angle of 70–120° from the vertical (Figs. 14, 16). The terminal cell of each of these filaments fuses with an adjacent medullary cell forming a secondary pit-connection (Figs. 14, 16). The resulting 1- to 2-celled interconnecting filaments elongate longitudinally along with cells of the axial filaments (Fig. 16). Axial filaments 1 cm from the apex range from 100–(550–750)–800 μm in length and from 3–(7–9)–14 μm in diameter.

In a mature thallus, systems of lateral filaments are composed of 9–13 orders of branches organized into approximately six layers (Figs. 16, 17). Cells of the outer cortex form a single layer and have one or two orders of branches. This layer is characterized by small, ellipsoidal, uninucleate pigmented cells which at most bear two branches. The inner cortex is composed of four cell layers having 4–5 orders of branches. Cells composing these layers are large, spherical to ovoid, and multinucleate. Cells of the innermost layer bear two branches while cells in the other three inner cortical layers bear either two or three branches per cell. The next layer of cells consists of only one order of branches and represents the transition from medulla to inner cortex. These cells, which are multinucleate, elongate, and at the same time somewhat expanded, bear only two

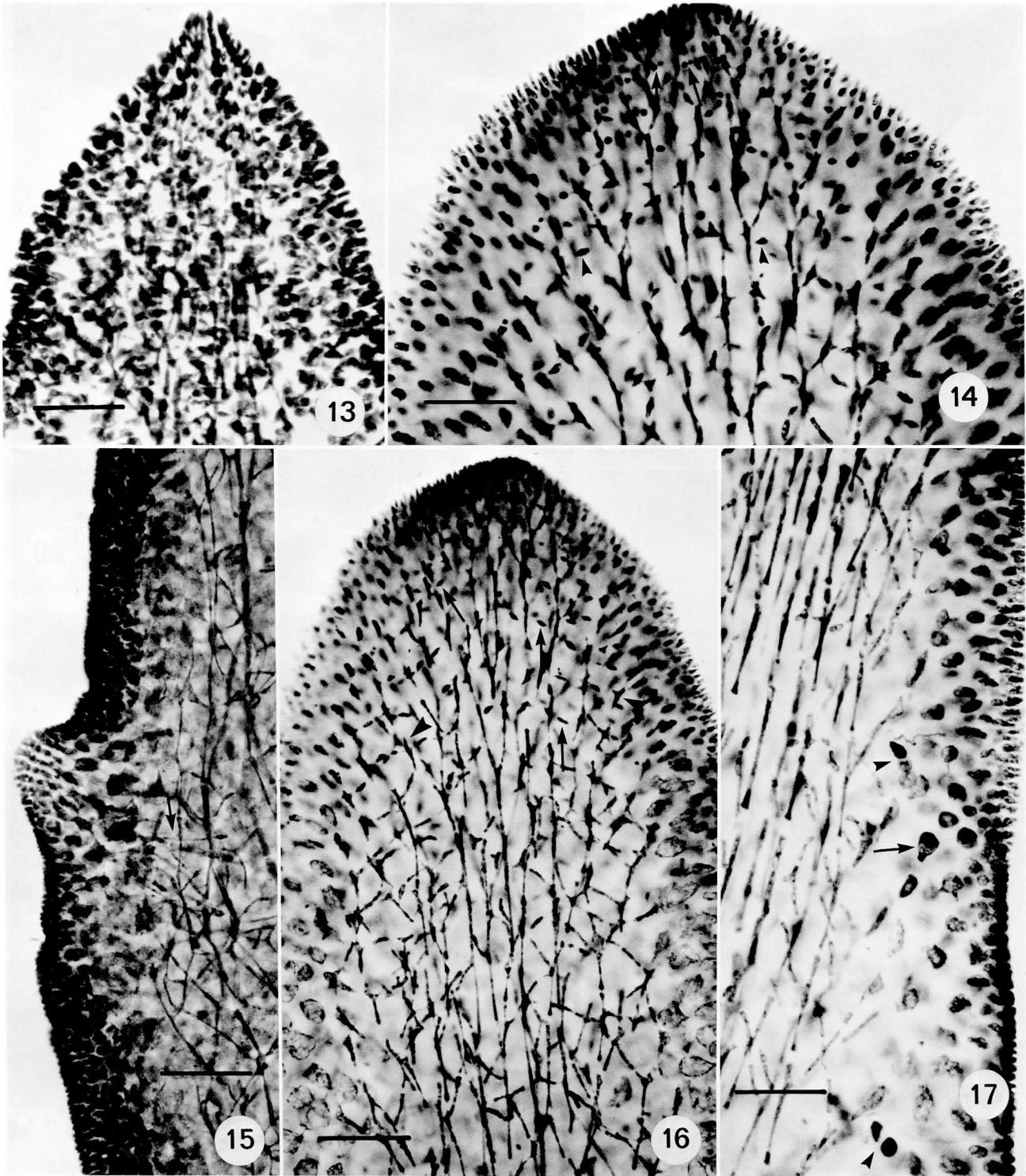
branches. The innermost layer lies within the medulla and consists of three to five orders of branches. The cells are elongate, multinucleate, and bear only two branches each. In a mature thallus the elongate cells of lateral branch systems are indistinguishable from true axial filaments.

When branches reach a diameter of 900–1000 μm , rhizoidal filaments are initiated from primary medullary filaments, interconnecting filaments and inner cortical cells (Fig. 21). Specimens of *Agardhiella subulata* that do not exceed 900 μm diameters do not form rhizoids. Rhizoidal filaments, which may ascend or descend several hundred micrometers through the thallus, are unbranched with diameters less than 1.7 μm , and form pit-connections at intervals throughout their length.

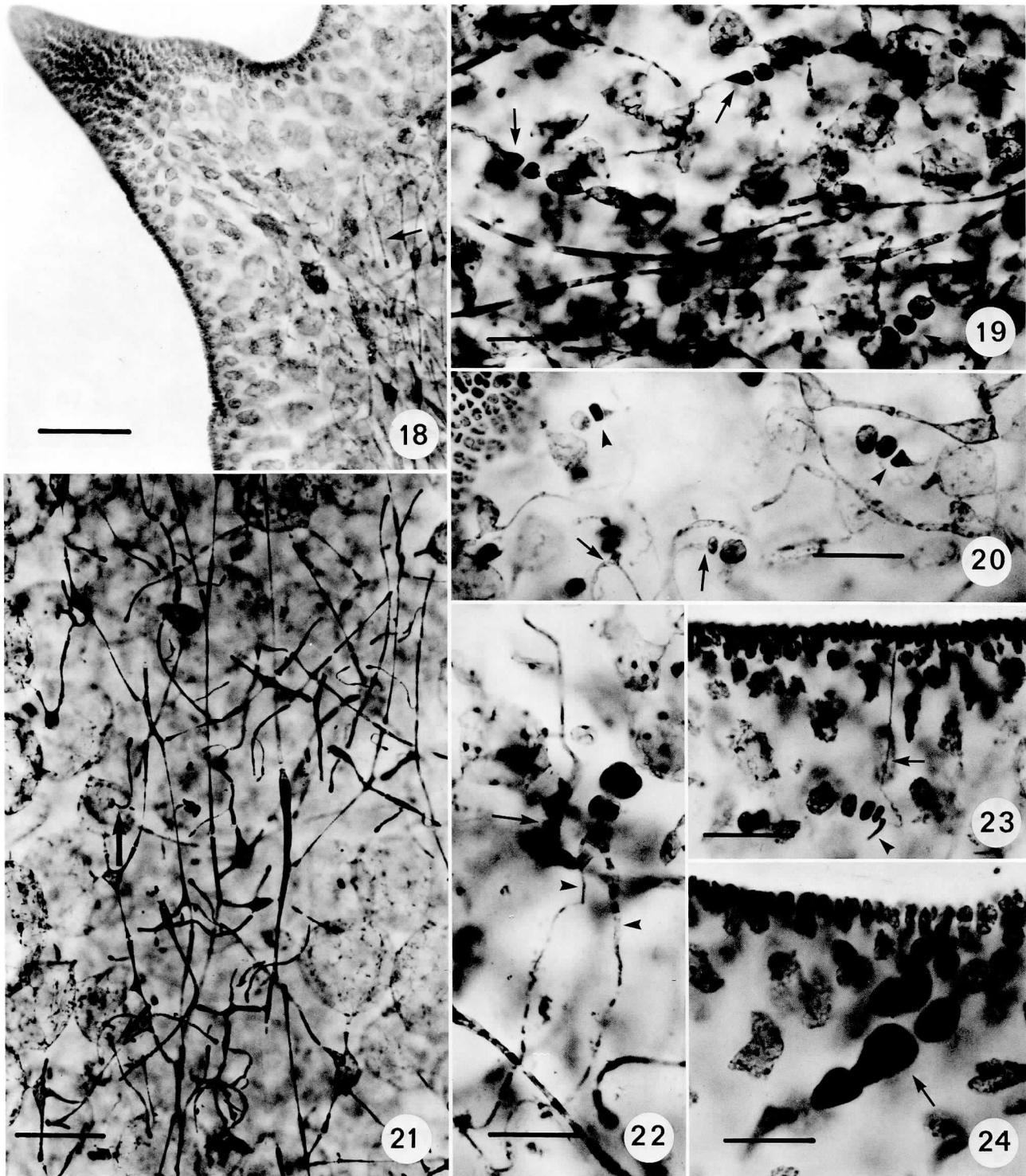
Branching of the thallus occurs adventitiously from a group of surface cortical cells which become meristematic, producing a primordium (Fig. 15). Inner cortical cells directly below the young primordium elongate and become the medullary cells in the transition area between the main axis and the primordium (Fig. 18). In addition, these cells cut off rhizoids which form secondary pit connections with the medullary cells of the main axis (Fig. 18).

Development of carpogonial branches and the auxiliary cell complex. Carpogonial branches begin to develop about ten cells behind the apex in female thalli. The supporting cell is a spherical to ovoid inner cortical cell of a lateral filament located two layers outside the transition layer (Fig. 17). The supporting cell bears, in addition to the carpogonial branch, two vegetative branches which extend to the surface. Carpogonial branches consist of three or occasionally four cells directed acropetally toward the interior of the thallus. The trichogyne is reflexed passing back through the cortex to the surface (Figs. 17, 22, 23). The first cell of the carpogonial branch is the largest, about 4 μm in diameter and is spherical to ovoid (Figs. 19, 20, 23). The hypogynous cell is usually wider than long (Figs. 19, 20) and may protrude to one side. The first two cells of the carpogonial branch are multinucleate (Fig. 19), while the conically-shaped carpogonium is uninucleate. Nuclei were not observed in any trichogynes.

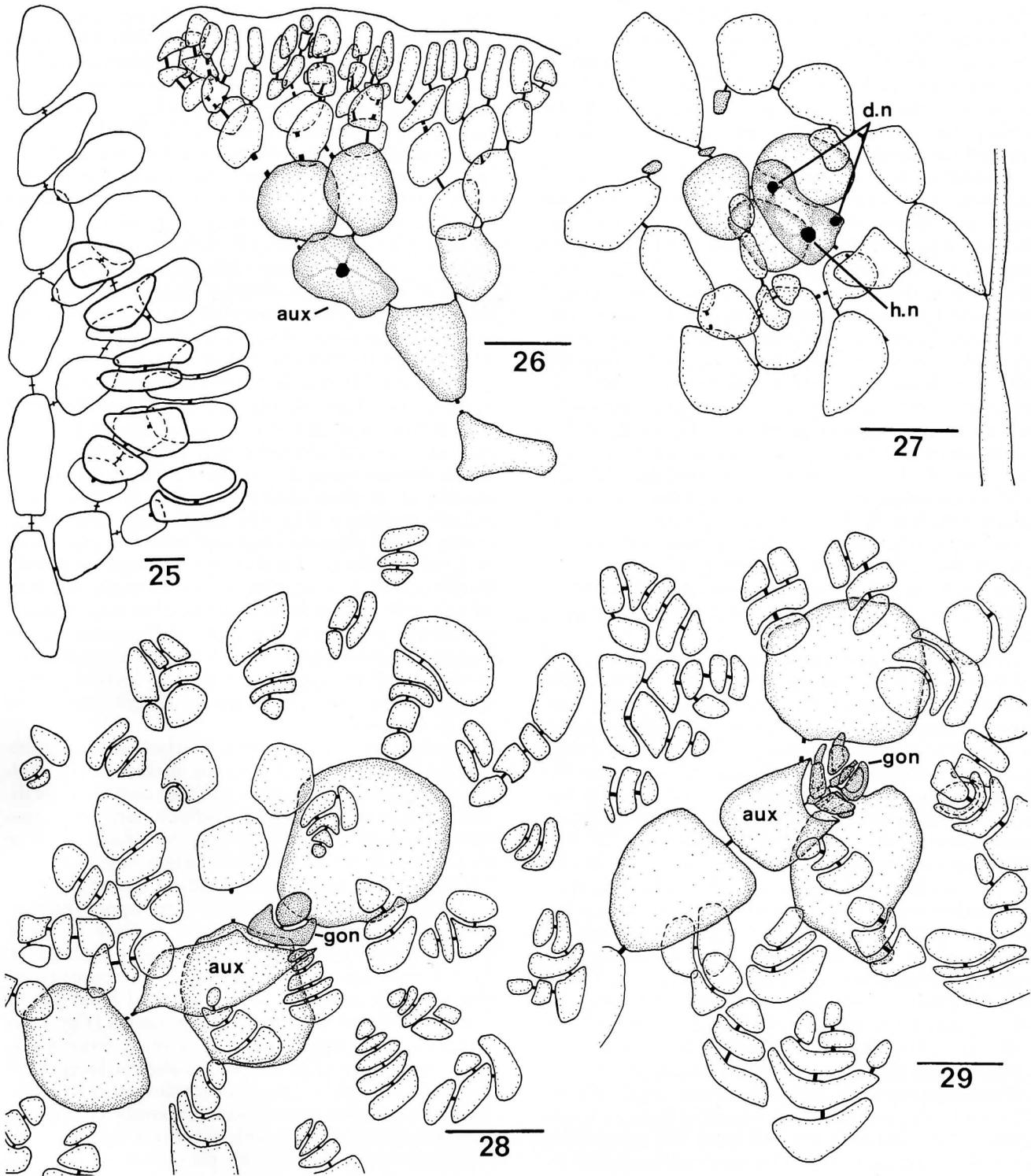
Auxiliary cells are first recognizable 15–20 segments behind the apex as darkly-staining inner cortical cells containing a single large centrally located nucleus (Fig. 17). Surrounding vegetative cells have by this time become multinucleate. Like the supporting cells of carpogonial branches, auxiliary cells are inner cortical cells of lateral filaments located two cells outside the transition layer (Figs. 24, 26). The vegetative cell bearing the auxiliary cell bears two branches, the auxiliary cell which itself bears two or three vegetative branches, and a vegetative branch (Fig. 26). As the uninucleate auxiliary cell matures, the multinucleate vegetative cells pit-connected to the auxiliary cell stain more darkly and enlarge from an average diameter of 22 μm (the



FIGS. 13–17. Vegetative development of *Agardhiella subulata*. FIG. 13. Surface view of slightly squashed tip. Scale = 40 μm . FIG. 14. Longitudinal section of apex. Arrows indicate 2-celled files, the terminal cells of which fuse with adjacent medullary cells to form interconnecting filaments (arrowheads). Scale = 40 μm . FIG. 15. Longitudinal section showing adventitious initiation of a lateral branch. Rhizoids issue from cortical cells beneath the lateral branch (arrow). Scale = 100 μm . FIG. 16. Median longitudinal section of a thallus apex showing axial filaments, diverging lateral filaments (arrowheads) and interconnecting filaments (arrows). Scale = 100 μm . FIG. 17. Longitudinal section of a female thallus showing the position of an auxiliary cell complex (arrow) and carpogonial branches (arrowheads). Scale = 60 μm .



FIGS. 18–24. *Agardhiella subulata*. FIG. 18. Grazing longitudinal section of a young branch showing rhizoid formation (arrow). Scale = 100 μm . FIG. 19. Three unfertilized carpogonial branches (arrows). Note the multinucleate condition of the inner cortical cells. Stained in Wittmann's haematoxylin. Scale = 60 μm . FIG. 20. Two fertilized (arrows) and 2 unfertilized (arrowheads) carpogonial branches. Arrow on left points to a pit-connection between one of the connecting filaments and the carpogonium. Degenerating trichogyne is opposite that arrow. Scale = 60 μm . FIG. 21. Longitudinal section adjacent to inner cortex showing production of secondary rhizoids (arrows) from inner cortical cells. Scale = 100 μm . FIG. 22. Fertilized carpogonial branch with two connecting filaments (arrowheads) and a trichogyne (arrow). Carpogonium is enucleate while other cells are multinucleate. Stained in Wittmann's haematoxylin. Scale = 40 μm . FIG. 23. Initiation of a connecting filament from a carpogonium (arrowhead). Trichogyne (arrow) protrudes through cortex. Scale = 60 μm . FIG. 24. Auxiliary cell complex before diploidization. Arrow indicates the auxiliary cell. Scale = 40 μm .



FIGS. 25-29. Camera lucida drawings of *Agardhiella subulata*. Abbreviations: aux = auxiliary cell; d.n = diploid nucleus; gon = gonimoblast; h.n = haploid nucleus. Scales = 30 μ m. FIG. 25. File of axial cells showing orthostichous arrangement of lateral files. FIG. 26. Auxiliary cell complex showing large, central, dark staining nucleus of the auxiliary cell. FIG. 27. Diploidized auxiliary cell containing two small diploid nuclei and central haploid nucleus. Surrounding vegetative cells are beginning to cut off short filaments. FIG. 28. Auxiliary cell and first two gonimoblast cells. Note files of cells cut off from surrounding vegetative cells. FIG. 29. Auxiliary cell and 2-tiered cluster of gonimoblast cells surrounded by files of cells forming the involucre.

size of other inner cortical cells) to $28\ \mu\text{m}$. The auxiliary cell also enlarges and forms a prominent beak (Figs. 27, 30, 31). Mature auxiliary cells measure about $38\ \mu\text{m}$ by $21\ \mu\text{m}$. The auxiliary cell and the three to four darkly-staining vegetative cells to which the auxiliary cell is pit-connected will be termed the auxiliary cell complex.

Diploidization of the auxiliary cell and development of gonimoblast. Trichogynes with attached spermatia were not observed and fertilization was not confirmed. Apparent fertilization results in the degeneration of the trichogyne (Figs. 20, 22, 23). Normally, two connecting filaments are seen issuing from the fertilized carpogonium, one with a pit-connection adjacent to the carpogonium and the other in open connection with the carpogonium (Figs. 20, 22). If only one connecting filament is formed it is without a pit-connection and non-septate throughout its entire length (Figs. 20, 23). Figure 22 shows a carpogonium bearing two connecting filaments and devoid of a nucleus. It is assumed that the diploid nucleus divides leading to septum formation and formation of a pit-connection with one of the connecting filaments and that the retained nucleus passes into the second connecting filament. Connecting filaments, which are unbranched, carry a diploid nucleus to a nearby or a distant auxiliary cell.

A connecting filament fuses with the internal end of an auxiliary cell and typically forms a bulge at the point of attachment (Fig. 30). Fusion of the connecting filament with an auxiliary cell is followed by a complex sequence of events. The presumed diploid nucleus divides and one nucleus moves to the beaked portion of the auxiliary cell, whereas the other remains in the auxiliary cell near the point of attachment of the connecting filament (Figs. 27, 31). The putative haploid nucleus remains in the center of the auxiliary cell (Figs. 27, 31). Following diploidization some of the vegetative cells in close proximity to cells of the auxiliary cell complex cut off initials which form secondary pit-connections with cells of the auxiliary cell complex (Fig. 27). Other nearby inner cortical and medullary cells begin to divide and form files of cells that grow toward the auxiliary cell complex. These files of cells are early stages in the development of an involucre that will ultimately surround the gonimoblast (Figs. 27, 28, 32). Once the involucre has begun to form, a single gonimoblast initial is cut off from the protruding end of the auxiliary cell. The gonimoblast initial divides transversely into two cells (Figs. 28, 32). Each of these cells divides further to form a 2-tiered, ovoid cluster of tightly packed gonimoblast cells (Figs. 29, 33). Cells of the auxiliary cell complex expand and the space created is occupied by the developing gonimoblast (Fig. 34). As the gonimoblast cells divide and branch, cells at the periphery fuse with nearby inner cortical cells. Vegetative cells of the involucre to which gonimoblast cells have fused

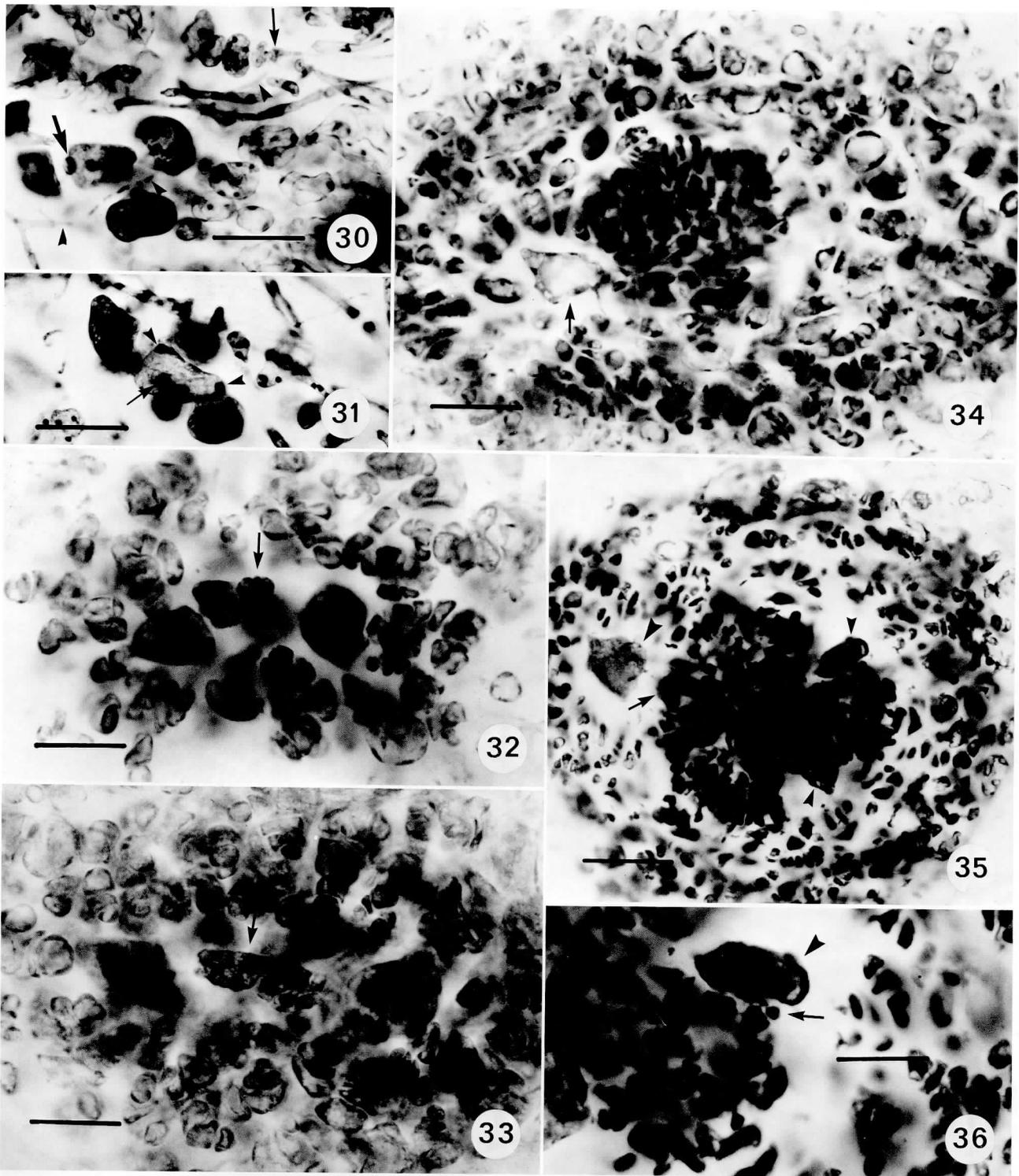
initiate new files of gonimoblast cells and these continue to grow outward (Figs. 35, 36, 38). The result is a progressive incorporation of vegetative cells of various origins into the central placenta of the cystocarp, the largest of these being cells of the original auxiliary cell complex (Figs. 35, 38, 39, 40).

An ostiole begins to form soon after the connecting filament has fused with the auxiliary cell. The outer cortical cells of the branch system containing the auxiliary cell begin to degenerate while the surrounding outer cortical cells divide to form a bulge with an opening over the young cystocarp (Fig. 37).

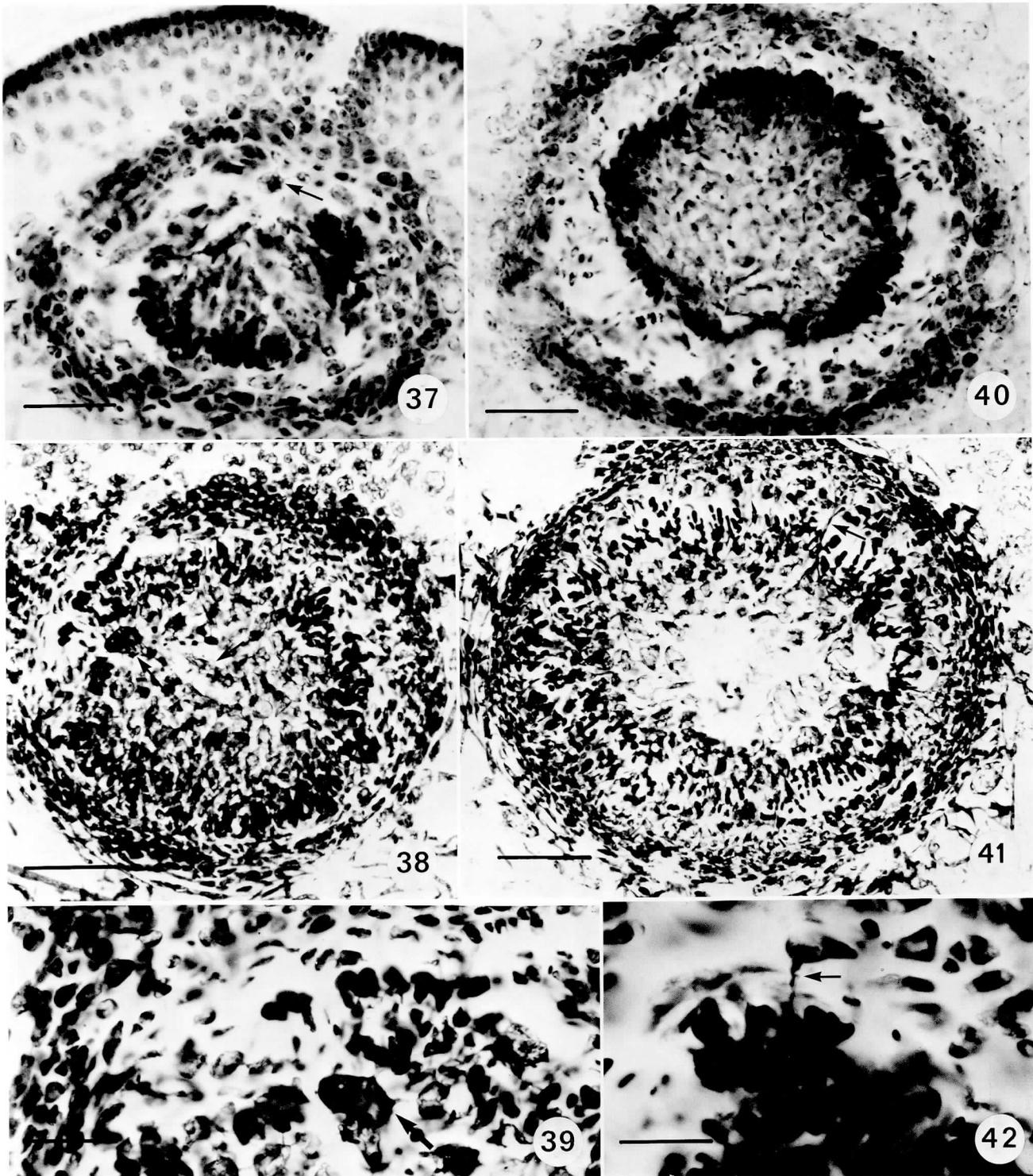
Sterile elongate gonimoblast cells radiating from the central placenta either fuse to, or form secondary pit-connections with cells of the involucre (Figs. 41, 42). Lightly staining cells at the periphery of the placenta cut off one to three darkly-staining gonimoblast cells (Figs. 44, 48). These cells bear terminal (Fig. 50) or short files of carposporangia (Fig. 49) or they may cut off horizontal files of gonimoblast cells which branch upward and bear carposporangia terminally or in short chains (Fig. 48). A section of a mature cystocarp (Fig. 43) shows large cells in the center of the placenta resulting from the expansion and vacuolization of a number of vegetative cells. Darkly-staining groups of carposporangia, separated by sterile gonimoblast filaments that have become connected to stretched involucreal filaments by fusion or secondary pit-connections, are located at the periphery of the placenta (Fig. 44). Mature carposporangia measure $34\text{--}47\ \mu\text{m}$ in length and $24\text{--}30\ \mu\text{m}$ in diameter.

Development of spermatangia. Patches of spermatangia are found scattered over the surface of the thallus of separate male plants. Surface cortical cells divide transversely to produce one or two spermatangial mother cells (Fig. 51). Each of these cuts off one or two spermatangia that measure $14\text{--}17\ \mu\text{m}$ in length and $6\text{--}7\ \mu\text{m}$ in diameter.

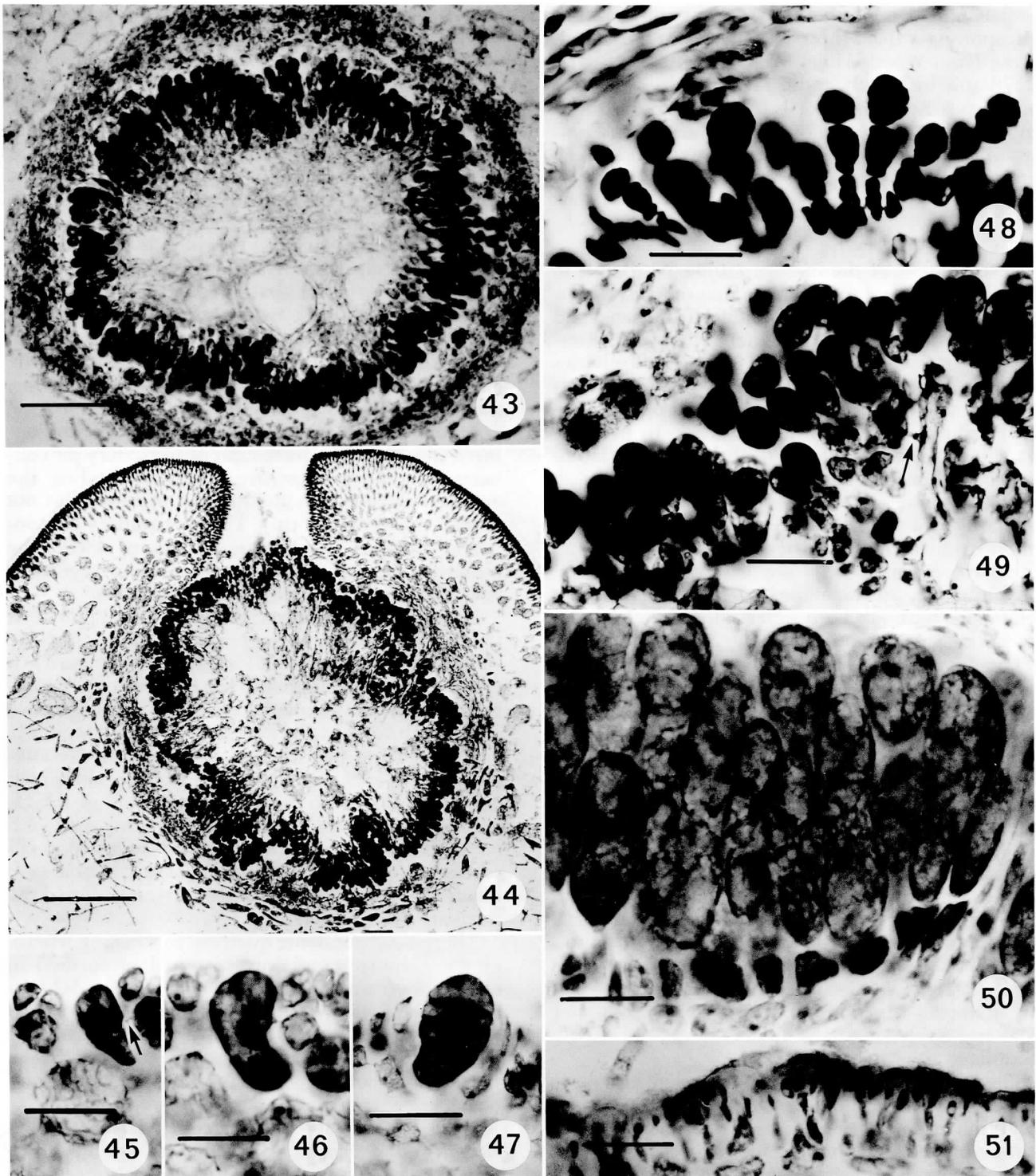
Development of tetrasporangia. Tetrasporangia are found scattered just beneath the surface in tetrasporic plants and occur everywhere except in branch tips and older main axes. Some tetrasporangial plants bear proliferations formed from the in situ germination of entire tetrasporangia (Fig. 1). A tetrasporangial initial is cut off laterally from a surface cortical cell (Fig. 45) and is slightly larger and stains more darkly than surrounding cortical cells. The young tetrasporangium expands basipetally into the cortex so that, with respect to its long axis, it is connected laterally by pit-connections to the bearing cell. A darkly-staining nucleus is apparent (Fig. 45). The bearing cell of a tetrasporangium next cuts off a derivative toward the surface (Fig. 46). At this stage the sporangium is ovoid with its broad end near the surface. Later the basal end expands and the sporangium becomes ellipsoid. The tetrasporangium undergoes successive zonate divisions parallel to its short axis. The pit-connection to the bearing cell remains lateral in position, just above the



FIGS. 30-36. Development of the carposporophyte of *Agardhiella subulata*. FIG. 30. Connecting filament (arrowheads) traceable from a carpogonium (small arrow) to an auxiliary cell where it produces a characteristic swelling (large arrow). Auxiliary cell is still uninucleate and surrounding cortical and medullary cells are multinucleate. A second connecting filament is seen extending from the carpogonium toward the right. Stained in Wittmann's haematoxylin. Scale = 40 μ m. FIG. 31. Auxiliary cell containing a large, central haploid nucleus (arrow) and two smaller diploid nuclei (arrowheads), one adjacent to the swelling at the point of fusion of the connecting filament and the other in the beak at the opposite end of the auxiliary cell. Scale = 40 μ m. FIG. 32. Auxiliary cell bearing a 2-celled gonimoblast (arrow) surrounded by dividing vegetative cells forming involucre. Scale = 40 μ m. FIG. 33. Auxiliary cell (arrow) with few-celled gonimoblast surrounded by involucre. Scale = 40 μ m. FIG. 34. Cell of the auxiliary cell complex (arrow) with compact radiating cluster of gonimoblast cells surrounded by involucre. Scale = 40 μ m. FIG. 35. Young cystocarp showing a dense cluster of darkly-staining gonimoblast cells surrounded by involucre. Auxiliary cell (arrow), its bearing cell (large arrowhead) and two other cells of the auxiliary complex (small arrowheads) are evident. Scale = 75 μ m. FIG. 36. One of the cells of the auxiliary cell complex (arrowhead) seen in Fig. 35 is shown pit-connected to gonimoblast cells (arrow). Scale = 25 μ m.



FIGS. 37-42. Development of the cystocarp of *Agardhiella subulata*. FIG. 37. Early stage showing a well developed ostiole. Arrow indicates a vegetative cell derived from a cell of the auxiliary cell complex involved in ostiole formation. Scale = 75 μ m. FIG. 38. Young cystocarp showing central placenta of fused vegetative and gonimoblast cells connected by pits, with darkly staining gonimoblast cells at the periphery surrounded by involucre. Large cells (arrows) are the auxiliary cell complex. Scale = 75 μ m. FIG. 39. Arrow indicates a vegetative cell of the placenta (visible in Fig. 38) connected by pits to gonimoblast cells. Scale = 40 μ m. FIG. 40. Central placenta of fused and pit-connected vegetative and gonimoblast cells and surrounded by involucre. Scale = 60 μ m. FIG. 41. Central placenta giving rise to short files of darkly-staining gonimoblast cells. Arrow indicates a sterile gonimoblast filament fusing with an involucral cell. Scale = 100 μ m. FIG. 42. A gonimoblast filament fused to an involucral cell (arrow). Scale = 25 μ m.



FIGS. 43-51. *Agardhiella subulata*. FIG. 43. Cystocarp showing a lacunate placenta with peripheral carposporangia surrounded by involucre. Scale = 175 μ m. FIG. 44. Mature cystocarp. Scale = 230 μ m. FIGS. 45-47. Development of tetrasporangia. FIG. 45. Young tetrasporangium with a lateral pit-connection. Scale = 25 μ m. FIG. 46. Maturing tetrasporangium. Scale = 25 μ m. FIG. 47. Mature, zonately divided tetrasporangium. Scale = 25 μ m. FIG. 48. Darkly-staining, branched gonimoblast cells giving rise to short files of carposporangia. Scale = 40 μ m. FIG. 49. Maturing files of carposporangia. Basal cells of files are pit-connected to the placenta (arrow). Scale = 40 μ m. FIG. 50. Mature, calvate-shaped, terminal carposporangia with pit-connections to gonimoblast cells. Scale = 25 μ m. FIG. 51. Spermatangia. Scale = 25 μ m.

median cleavage of the tetrasporangium. Mature tetrasporangia from three localities were measured. Those from Woods Hole, Massachusetts, measured 54–78 μm in length and 37–44 μm in diameter; those from Beaufort, North Carolina 47–57 μm in length and 27–34 μm in diameter; those from Pompano Beach, Florida 54–64 μm in length and 34–40 μm in diameter.

DISCUSSION

Development of the mature multiaxial thallus in *Agardhiella subulata* differs from that of *Solieria chordalis*, the type genus of the family. In *Solieria* and the closely related uniaxial genera *Rhabdonia*, *Areschougia* and *Melanema*, each apical cell divides obliquely producing a subterminal cell which cuts off a periaxial cell. Successive periaxial cells are rotated around the axial file and divide to produce branched cortical filaments (Gabrielson and Hommersand 1982). In contrast, each apical cell in *A. subulata* obliquely cuts off a single derivative which functions as a primary axial cell. A single periaxial cell is produced by the third cell below the apex and successive periaxial cells are orthostichous (Kylin 1928 and Fig. 25 this paper). Details of apical development have not been well studied in other genera in the Solieriaceae.

The formation of short 2- to 3-celled interconnecting filaments is characteristic of *Agardhiella* and *Sarcodiotheca* (Gabrielson 1979) and also of *Solieria* (Gabrielson and Hommersand 1982) within the Solieriaceae. Certain genera in the multiaxial families Acrotylaceae (Kraft 1977a, *Acrotylus* and *Ranavalona*) and Dicranemataceae (Kraft 1977b, *Dicranema*), and the uniaxial family Mychodeaceae (Kraft 1978, *Mychodea*), also exhibit interconnecting filaments. Kraft termed these structures cross-connector cells or filaments. In the uniaxial family Mychodeaceae they serve to link adjacent cells of the axial strand and may also form secondary pit-connections to cortical cells and other cross-connector cells (Kraft 1978). Likewise in *Agardhiella*, interconnecting filaments function primarily to bind together axial and stretched lateral filaments composing the medulla at the thallus apex.

There is agreement among the many investigators concerning the origin, development and nuclear condition of cells of the carpogonial branch. Reports of the number of connecting filaments formed from each carpogonium varies somewhat with Osterhout (1896) reporting one to three, Kylin (1928) two or three, Wynne and Taylor (1973) one to several and our observations of one or two. Single connecting filaments emanating from carpogonia are uncommon and we have observed no more than two from any single carpogonium. Our observations on the development of the auxiliary cell complex concur with those of Osterhout (1896) and Kylin (1928).

The inner cortical cell that is transformed into an auxiliary cell is homologous with the supporting cell

of a carpogonial branch. Therefore, in each lateral branch system beginning with the outermost medullary cell and moving toward the cortex only a single reproductive structure, either an auxiliary cell or a supporting cell of a carpogonial branch may be present. The auxiliary cell and the supporting cell of the carpogonial branch differ in one important aspect: the auxiliary cell is uninucleate at maturity, whereas the supporting cell, like all other inner cortical cells, is multinucleate.

The term auxiliary cell complex is used here to distinguish those darkly-staining cells pit-connected to the auxiliary cell that are physiologically and functionally different from the surrounding vegetative cells. Functionally, these cells together with the auxiliary cell appear to supply nutrients for the early stages of gonimoblast development and they maintain their orientation with respect to one another into the late stages of cystocarp development (Fig. 38). The formation of secondary pit-connections among vegetative cells surrounding the auxiliary cell prior to gonimoblast initiation has not been reported previously. These secondary pit-connections help to stabilize the position of cells of the auxiliary cell complex and surrounding vegetative cells as the gonimoblast grows and expands.

Osterhout's (1896) description of development of the involucre does not agree with our own observations. Osterhout (1896) reported that pericarp (=involucre) development began prior to "conjugation with the auxiliary cell," that the vegetative cells which formed the pericarp divided irregularly and away from the auxiliary cell and that the auxiliary cell as well as the surrounding vegetative cells cut off files of cells. In fact, development of the involucre follows fusion of a connecting filament with an auxiliary cell and proceeds from vegetative cells surrounding the auxiliary cell complex. These cells divide and exhibit apical growth directed toward the auxiliary cell complex.

There has been some question concerning whether the carposporangia are terminal or formed in chains in *Agardhiella subulata*. Schmitz (in Schmitz and Hauptfleisch 1896) and Kylin (1928) report terminal carposporangia, Osterhout (1896) reports chains of carposporangia and Harvey (1853) reports chains of carposporangia as well as terminal ones. Recently, Abbott (1978) reported chains of four to six carposporangia in *A. subulata* (as *Neoagardhiella baileyi*). Like Harvey, we have observed terminal as well as 3- to 4-celled unbranched files of carposporangia.

Kylin (1928, fig. 45B) shows a periclinally divided surface cortical cell giving rise to a tetrasporangium. In all cases we have observed only tetrasporangia with lateral pit-connections. It is possible that Kylin confused a darkly staining cortical hair initial, common on young plants of *A. subulata*, with a tetrasporangial initial. Measurements of tetrasporangia from three localities along a north-south gradient showed that the largest tetrasporangia were in

northern plants, but measurements from all three localities overlapped.

Distribution. There has been some question regarding the distribution of *Agardhiella subulata* following its recognition as an entity distinct from *Solieria tenera*. Wynne and Taylor (1973) characterized *A. subulata* (as *Neoagardhiella baileyi*) as primarily a temperate species ranging northward to southern New England and *S. tenera* as a plant of tropical waters, although noting the occurrence of both species in the Gulf of Mexico. *A. subulata* has been reported from Canada (South 1976, incorrectly as *Solieria tenera*), although its northern limit is generally considered to be Cape Cod, Massachusetts. Plants from localities in Massachusetts grow to 20 cm in height and generally have narrow branches less than 2 mm in diameter with long attenuate apices (Fig. 8). From Long Island Sound south to Indian River, Florida, *A. subulata* is a more conspicuous member of the intertidal flora and can also occur subtidally. *A. subulata* also occurs subtidally along the east coast of southern Florida where it is collected in the drift. It is found intertidally along the west coast of Florida and has been reported from Texas (Wynne and Taylor 1973). Plants from the above localities exhibit the full range of morphological variation found in the species, depending on the habitat in which the plants occur (Figs. 1-5, 8, 10, 11).

The distribution of *A. subulata* overlaps that of *Solieria tenera* from North Carolina south into the Caribbean Sea and at Port Aransas, Texas in the Gulf of Mexico. In North Carolina *S. tenera* is found only in deep water (Schneider 1976) whereas *A. subulata* is a common intertidal plant from April through July. *Agardhiella subulata* is found in numerous localities in the Caribbean Sea including Cuba (Fig. 12), Jamaica, Puerto Rico, St. Croix, Virgin Islands (Fig. 9), Dominica, Tobago and Cubagua Island, Venezuela (Fig. 6). Specimens from the Caribbean Sea have a size range similar to those from Massachusetts, but lack the long attenuated apices generally characteristic of northern plants. The Caribbean plants generally have 2 to 3 orders of branching and the diameter of the main axis is usually about 2 mm, the same as that of the branches. One specimen from Pernambuco (Recife) Brazil is *A. subulata* (Gabrielson 1980), but reports of *A. tenera* from southern Brazil are referable to *Solieria tenera* (Joly 1965, Cordiero-Marino 1978).

Agardhiella exhibits a combination of vegetative and reproductive features that separates it from the uniaxial (*Rhabdonia*, *Erythroclonium*, *Areschougia* and *Melanema*) and multiaxial (*Solieria* and *Callophycus*) genera that have been placed in the tribes Solierieae and Areschougieae (Gabrielson and Hommersand 1982). The characters include: 1) lateral filaments orthostichous, periaxial cells formed successively in vertical files, 2) auxiliary cell complex of darkly-staining cells recognizable prior to diploidization, 3) typically two connecting filaments, one with a pit-

connection and the other in open connection with the carpogonium, 4) files of involuclral cells from surrounding vegetative cells that grow toward the auxiliary cell following diploidization, 5) a placenta of fused and pit-connected gonimoblast and vegetative cells in the center of the cystocarp, and 6) tetrasporangia with lateral pit-connections. We believe that *Agardhiella* stands sufficiently apart from the tribes Solierieae and Areschougieae to warrant establishment of a new tribe, the Agardhielleae, to accommodate it.

Agardhielleae

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Multiaxial; lateral filaments orthostichous, the lateral initials formed successively in vertical files; carpogonial branches generally without sterile cells; an auxiliary cell complex of darkly-staining cells recognizable prior to diploidization; typically two connecting filaments, one with a pit-connection and the other in open connection with the carpogonium; files of involuclral cells from surrounding vegetative cells that grow inwardly toward the auxiliary cell following diploidization; placenta of fused gonimoblast and vegetative cells with pit-connections in the center of the cystocarp; tetrasporangia with lateral pit-connections.

Plantae multiaxiales; filamenta lateralialia orthostichosa, initia lateralialia in ordinibus verticalibus successive formata; rami carpogoniales plerumque sine cellulis sterilibus; cellula auxiliariae atque cellulae eae consociatae, omnibus maxime tinctibilibus, ante diploidizationem agnoscibiles; filamenta coniungentia typice duo, uno foveo-colligationem habente, altero cum carpogonio aperte connexo; ordines cellularum involuclralium e cellulis vegetativis circumdantibus enascent auxiliarem versus post diploidizationem introrsus crescunt; placenta, in centro cystocarpi e gonimoblasto atque cellulis vegetativis, omnibus se coniunctis atque foveis connexis, composita; tetrasporangia foveo-colligationes laterales habentia.

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