

CHARACTERIZATION OF *SCHIZOSERIS CONDENSATA*, SCHIZOSERIDEAE TRIB. NOV.  
(DELESSERIACEAE, RHODOPHYTA)<sup>1</sup>

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ABSTRACT

The Myriogramme group of Kylin contains two distinct clusters of genera that merit recognition at the tribal level. We previously established the tribe Myriogrammeae, and in this paper we erect the Schizoserideae based on a study of the type species of Schizoseris, *S. laciniata* (= *S. condensata*), from the southern hemisphere. The Schizoserideae is characterized by 1) marginal and diffuse intercalary meristems; 2) nuclei initially arranged in a plate in the median plane in meristematic and mature cells; 3) chloroplasts one to few, lobed or dissected; 4) microscopic veins absent; 5) procarps scattered, formed singly on either side of the blade with cover cells absent and consisting of a one- to two-celled lateral sterile group, a one- to two-celled basal sterile group, and a four-celled carpogonial branch in which the trichogyne passes beneath the lateral sterile group and emerges anterior to it; 6) auxiliary cell diploidized by a connecting cell cut off posteriolaterally from the fertilized carpogonium; 7) gonimoblast initial cut off laterally from one side of the auxiliary cell and giving rise to unilaterally branched gonimoblast filaments bearing carposporangia in branched chains; 8) gonimoblast fusion cell highly branched, candelabra-like, incorporating all but the basalmost cells of the carposporangial chains and radiating through the central cells in the floor of the cystocarp; 9) spermatangial and tetrasporangial sori formed from surface cells in both monostromatic and polystromatic portions on both sides of the blade; and 10) tetrasporangia formed primarily from cortical rather than from central cells. The Schizoserideae presently includes *Schizoseris* Kylin, *Neuroglossum* Kützing, *Abroteia* J. Agardh, and *Polycoryne* Skottsberg in Kylin and Skottsberg.

**Key index words:** Ceramiales; Delesseriaceae; morphology; Schizoserideae trib. nov.; Schizoseris; Rhodophyta; subantarctic; systematics; taxonomy

We recently proposed that the Myriogramme group of Kylin (1924:53) contains two distinct clusters of genera that merit recognition as separate tribes: one centered around *Myriogramme* Kylin (1924:55) and the other around *Schizoseris* Kylin (1924:67) (Hommersand and Fredericq 1997). In our previous paper, we established the tribe Myriogrammeae. Here we propose the Schizoserideae trib. nov., based on an investigation of the type species of *Schizoseris*, *S. laciniata* Kylin (= *Schizoseris con-*

*densata* (Reinsch) Ricker) from Chile and an examination of related taxa.

*Schizoseris* Kylin was established upon *Delesseria laciniata* Kützing (1866:8, pl. 19) from the Strait of Magellan. Ricker (1987) replaced *Schizoseris laciniata* Kylin with *Schizoseris condensata* (Reinsch) Ricker (1987:283) based on *Delesseria condensata* Reinsch (1888:150) from South Georgia Island, because *D. laciniata* Kützing is a later homonym of *D. laciniata* (Hudson) Greville (1824:293), the basionym for *Callophyllis laciniata* (Hudson) Kützing 1843. The synonymy of *Schizoseris condensata* is given by Ricker (1987) and Papenfuss (1964). The seven remaining species of *Schizoseris* reported from the southern hemisphere are exceedingly polymorphic. Ricker placed all but one of these in synonymy under *Schizoseris dichotoma* (J. D. Hooker et Harvey) Kylin (1924:68), including *Myriogramme multinervis* (J. D. Hooker et Harvey) Kylin (1924). Subsequently, Wynne (1989) showed that the earliest available name for *Schizoseris davisii* (Hooker et Harvey) Kylin 1924, one of the species Ricker had subsumed under *S. dichotoma*, is *Schizoseris griffithsia* (Suhr) Wynne 1989 from Chile.

In this paper, we investigate the vegetative and reproductive development of material of *Schizoseris condensata* from Chile and establish the tribe Schizoserideae to include *Schizoseris* Kylin 1924, *Neuroglossum* Kützing 1843, *Abroteia* J. Agardh 1876, *Drachiella* Ernst et J. Feldmann 1957, and provisionally *Polycoryne* Skottsberg in Kylin and Skottsberg 1919.

MATERIALS AND METHODS

Morphological observations of *Schizoseris condensata* were made on drift specimens from Playa Grande, Niebla, 25 km west of Valdivia, Prov. Valdivia, Chile, collected by M. Hommersand, 3 January 1979. Additional drift collections came from Campo Bolnearo, near Maullin, Prov. Llanquihue, Chile, collected by M. Hommersand, 7 January 1979. Whole-mount and sectioned material were stained either with aniline blue and mounted in Karo® syrup or glycerine or were treated with Wittmann's aceto-iron-hematoxylin-chloral hydrate (Wittmann 1965) and mounted in 50% Hoyer's mounting medium or transferred to Piccolyte® as described by Hommersand and Fredericq (1992, 1997). Drawings were made with a camera lucida and photographs were taken with a Zeiss photomicroscope III. Herbarium abbreviations follow Holmgren et al. (1990).

RESULTS

*Schizoseris* Kylin (1924:67)

**Description:** Plant body attached by a primary basal disc, erect to 40 cm tall; stipe short to long, sometimes rhizomatous, or wanting; blade simple, entire or variously lobed, lacerate, or deeply cleft to base of blade, sometimes proliferous. Microscopic veins absent. Macroscopic nerves present, simple and ba-

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sal, or subdichotomously branched and extending through the blade, sometimes almost to the margin. Blade initially monostromatic, becoming distromatic, tristromatic, or polystromatic behind margin, near stipe or base, or upon formation of macroscopic nerves. Nerve and stipe thickenings formed by a combination of periclinal and anticlinal divisions and consisting of branched filaments radiating toward the thallus surface. Internal rhizoids absent. Thallus margin typically composed of a mixture of triangular and rectangular cells, entire or minutely serrulate. Growth diffuse, by marginal and intercalary meristems, the cell divisions irregularly rectangular to oblique producing cells of varying shapes and sizes. Surface cells seemingly containing a single parietal chloroplast that is variously lobed, convoluted, fenestrate, or dissected into ribbons; inner cells of polystromatic regions often containing several chloroplasts; chloroplast probably metastable, breaking up and fusing under different conditions. Nuclei one to many, arranged in a plate across middle of cell in meristematic and young mature cells, either platelike or variously dispersed in mature cells in older tissues. Primary and secondary pit-connections prominent, initially median, and typically with one pit-connection between adjacent cells; additional minute secondary pit-connections formed at surface of blade in some, infrequent to abundant according to species. Spermatangia in separate or aggregated sori on monostromatic or polystromatic parts of thallus. Procarps formed singly on one or the other side of the thallus, but not opposite one another, circular in outline consisting of a supporting cell bearing a large, one-celled (rarely two-celled) lateral sterile group, a strongly curved four-celled carpogonial branch in which the trichogyne traverses beneath the lateral sterile group emerging anterior to it, and a small, one-celled basal sterile group. Auxiliary cell broader than tall, diploidized by the second (proximal) connecting cell and dividing vertically into a lateral gonimoblast initial and residual auxiliary cell containing both haploid and diploid nuclei; gonimoblast filaments at first developing unilaterally in an arc to one side, later radiating in all directions and bearing carposporangia in unilaterally branched chains; cells of the carpogonial branch fusing into a single, sickle-shaped cell before degenerating; supporting cell first fusing with the residual auxiliary cell and the second sterile group, followed by the primary gonimoblast cell and central cell, the fusion cell then expanding through incorporation of inner gonimoblast cells and cells in floor of cystocarp, later becoming candelabra-like with the incorporation of nearly all gonimoblast cells not transformed into carposporangia; pericarp four to six cell layers thick with the ostiole typically off center overlying the first sterile group, sometimes with a collar or short beak. Tetrasporangia formed in small, separate circular sori, or the sori aggregated and confluent; primary tetrasporangia

arising from inner cortical cells and disposed in two layers covered by cortical cells and superficial cells, or developing on nerves on either side of thallus and then covered by a newly formed cortex on one side only; secondary tetrasporangia also arising from cortical cells, often the ones closer to the thallus surface. Division of tetrasporangia tetrahedral.

*Schizoseris laciniata* Kylin (= *S. condensata* (Reinsch) Ricker (1987:283))  
(Figs. 1–62)

Description: Thallus stipitate, erect from a compact disc to 45 cm high, reddish orange to red-brown to purplish black; blade monostromatic with alternately to subdichotomously branched polystromatic nerves that extend almost to the blade tips and margins; highly lacinate with splits developing inside the margins and between the nerves, and with small leaflets commonly proliferating from the surfaces and eroded margins of the nerves; margins smooth or minutely serrulate with apiculate marginal cells. Spermatangia covering the surfaces of blades or borne on small leaflets proliferating from the nerves. Cystocarps borne on or alongside the macroscopic nerves, hemispherical, each with a raised collar and slitlike ostiole; gonimoblasts with candelabra-like fusion cells and radiating fusion processes extending along the floor of the cystocarp; carposporangia subspherical, borne in simple or unilaterally branched chains along the sides or at the ends of the branched fusion cell. Tetrasporangia formed in irregularly shaped sori covering monostromatic and polystromatic portions on both sides in upper parts of blade (Mendosa 1969, 1974, Ricker 1987).

Genetype: *Delesseria laciniata* Kützing 1866:8, pl. 19 (non *D. laciniata* (Hudson) Greville 1824), Strait of Magellan, L.

Syntype: *Delesseria condensata* Reinsch 1888:150, South Georgia 'Nordstrand der Landzunge' (Will, Feb. 1883); M, unnumbered specimen (see Ricker 1987:285).

Nomenclatural synonyms: *Delesseria condensata* Reinsch 1888:150, *Nitophyllum condensatum* (Reinsch) Skottsberg 1923:47.

Taxonomic synonyms: *Schizoseris laciniata* Kylin 1924:67, *Nitophyllum affine* Reinsch 1888:153, *Myriogramme macquariensis* Zinova 1963:63.

Specimens examined: *Schizoseris condensata* (Reinsch) Ricker, drift, Playa Grande, Niebla, Prov. Valdivia, Chile, female & tetrasporic, coll. M. H. Hommersand, 3.i.1979; Campo Bolnearo, 2 km SW of Maullin, Prov. Llanquihue, female & tetrasporic, coll. M. H. Hommersand, 7.i.1979.

Specimens of other taxa examined: *Schizoseris davisii* (J. D. Hooker et Harvey) Kylin 1924 [= *S. griffithsia* (Suhr) Wynne 1989]: syntypes of *Delesseria davisii* J. D. Hooker et Harvey, St. Martens Cove, Cape Horn, BM; drift, 8 km northeast of Punta Arenas, Estrecho de Magallanes, Prov. Magallanes,

Chile, female, coll. M. H. Hommersand, 9.i.1979; *Schizoseris dichotoma* (J. D. Hooker et Harvey) Kylin 1924: syntypes of *Delesseria dichotoma* J. D. Hooker et Harvey, No. 89, Auckland I.; No. 90, Auckland I. sterile & female, XII. 1840; No. 50, Campbell I, tetrasporic; other material, on the beach, Ruapuke, Foveaux Strait, New Zealand, female & tetrasporic, coll. D. Lyle, i.1851; Preservation Harbor, West Coast, Middle I., New Zealand, tetrasporic, coll. D. Lyle, i.1851; Chalky Bay, west coast, New Zealand, female, coll. D. Lyle, ii.1851; as *Delesseria davisii*, on the beach, Ruapuke, Foveaux Strait, New Zealand, female & tetrasporic, coll. D. Lyle, i.1851; Moses Nugget, Ringa Ringa, Patterson Inlet, Stewart I., New Zealand, male?, female & tetrasporic, coll. M. H. Hommersand 4.xii.1974; Pilot Beach, Taiaroa Heads, Otago Peninsula, New Zealand, female and tetrasporic, coll. M. H. & F. C. Hommersand 16.x.1974. *Myriogramme multinervis* (J. D. Hooker et Harvey) Kylin 1924: syntypes of *Nitophyllum multinerve* J. D. Hooker et Harvey, St. Martens Cove, Cape Horn; on the beach, Berkeley Sound, E. Falkland I., coll. D. Lyle, 1842; other material, Drift, Playa Grande, Niebla, Prov. Valdivia, Chile, female & tetrasporic, coll. M. H. Hommersand, 3.i.1979. *Myriogramme gattyana* (J. Agardh) Kylin 1924: syntypes of *Nitophyllum gattyanum* J. Agardh, from the Derwent, Hobart, Tasmania, Australia, LD:30615 (female), 30616 (tetrasporic); Evening Cove, Patterson Inlet, Stewart I., New Zealand, female and tetrasporic, coll. M. H. Hommersand, 5-6.xii.1974. *Neuroglossum binderianum* Kützinger 1843: Atlantic side, 5 km N of Cape of Good Hope, Cape Province, South Africa, female & tetrasporic, coll. M. H. Hommersand, 9.xii.1977. *Abroteia orbicularis* J. Agardh 1976: New Zealand, tetrasporic, coll. Berggren; LD: 26188 (partim); Atia Point, Kaikoura Peninsula, South Island, New Zealand, on *Carpophyllum machalocarpum*, female & tetrasporic; coll. M. H. Hommersand, 12.x.1974; *Nitophyllum suborbiculare?* Harvey: Blind Bay, Cook Strait, New Zealand, tetrasporic, coll. D. Lyle, vii. 1849; Colenso No. 3164, New Zealand, BM ex TCD.

**Vegetative growth.** Freshly collected plants of *Schizoseris condensata* were rose-red to purplish brown in color, relatively soft in texture, highly lacinate, and feathery in appearance with small bladelets occasionally proliferating from the midribs (Figs. 1, 3). The primary branching was irregularly subdichotomous, evidently due to the formation of deep laciniae accompanied by rapid growth. Tips of blades were variable in shape ranging from acute to broadly rounded. Blades were monostromatic except for the multistratose midribs and lateral nerves. Midribs and nerves differentiated acropetally but did not reach the tips or margins (Fig. 2), except secondarily as a result of abrasion.

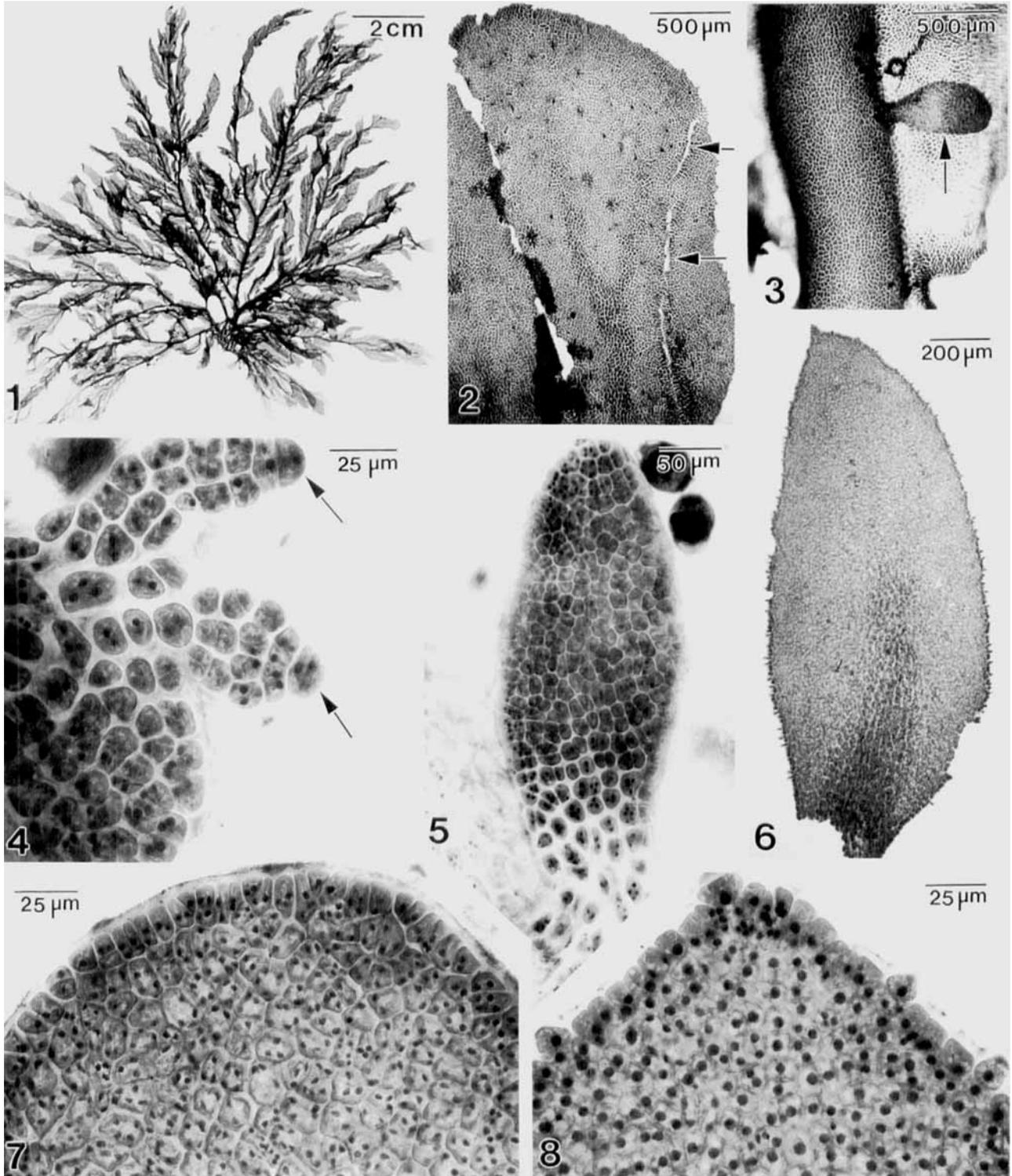
Growth takes place primarily through the activity of an intercalary meristem, with the marginal meristem functioning primarily to repair breaks that result from thallus abrasion or the formation of laci-

nae. Margins of small proliferous bladelets are entire (Figs. 3-5, 7), but become minutely serrulate in older bladelets (Fig. 6) and at the tips and margins of adult thalli (Figs. 2, 8-11). Microscopic teeth formed along the margin are composed of triangular-shaped cells that resemble apical cells or may consist of short files 2-3 cells long (Figs. 8-11). Laciniae and parts of a blade being sloughed originate as slits within the blade bordered by newly formed marginal meristems (Fig. 2). Lacination occurs when a slit extends outwardly to the margin and inwardly toward the midrib, usually alongside lateral nerves.

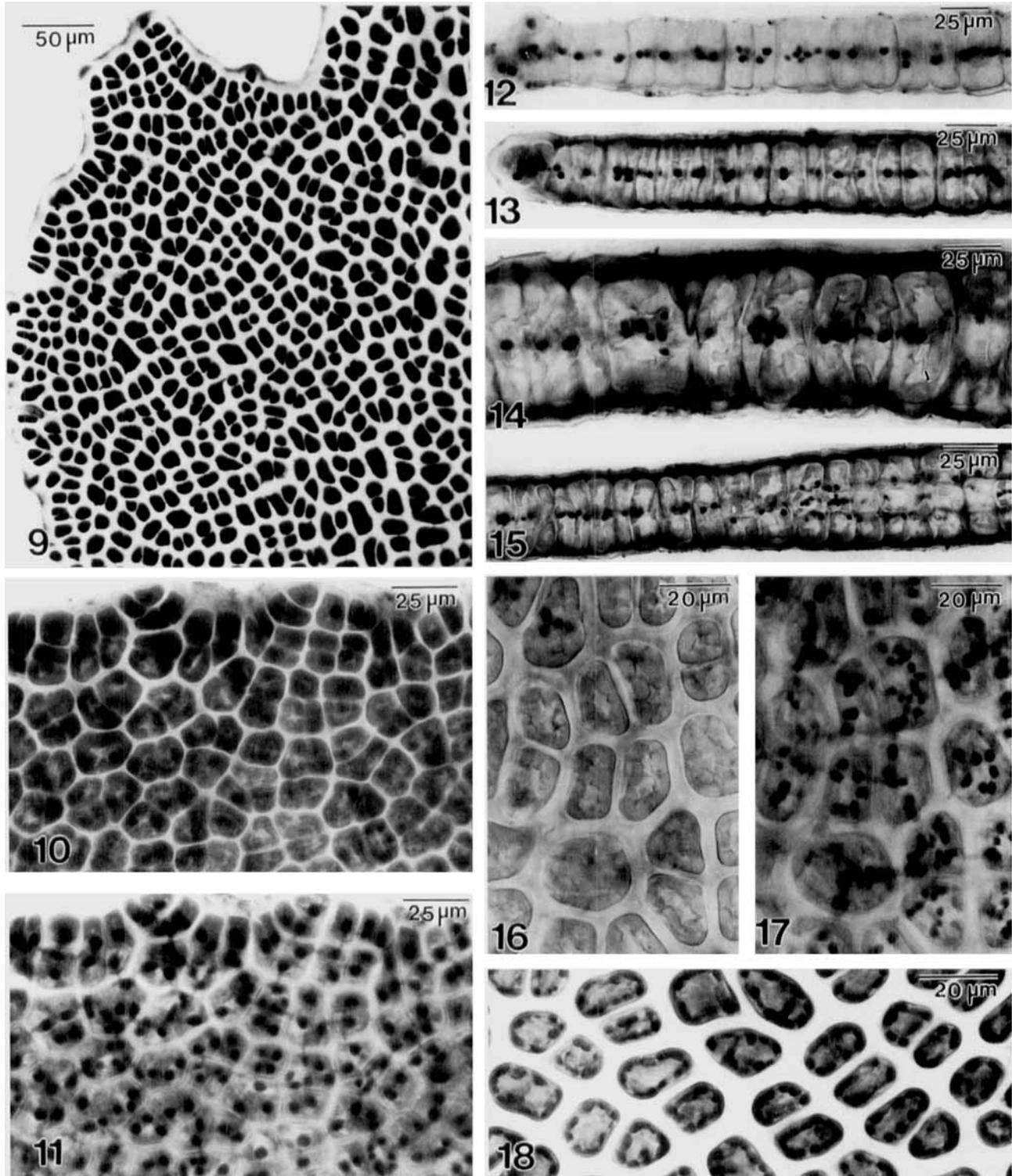
Apical cells are sometimes seen at the tips of tiny proliferations that occur along midribs in older thalli (Fig. 4). Unlike the apical initials found in genera such as *Phycodrys* Kützinger, which are invariably uninucleate, these cells may be uninucleate or binucleate and do not persist as organizing elements for very long. Monostromatic parts of a thallus are composed almost entirely of meristematic areas in which the cells continue to divide throughout the life of a blade. This is dramatically illustrated in Figure 9, which shows the basal portion of a blade in which the innermost cells appear to be dividing as actively as those close to the margin. Marginal initials are typically uninucleate or binucleate, are triangular in shape, and are often organized in short, branched files (Figs. 7, 8, 11). Cells of the intercalary meristem are uninucleate, binucleate, or multinucleate and form meristematic patches in which cell divisions often occur successively at right angles to one another or are irregular (Fig. 9). Viewed from above, the chloroplasts are situated toward the surface on both sides (Figs. 10, 16, 18) and the nuclei lie in the median plane (Figs. 11, 17). Seen in cross-section, the nuclei are strictly median in young tips (Fig. 12), older margins (Fig. 13), and intercalary regions in monostromatic parts of the blade (Fig. 14). Like the nuclei, primary and secondary pit connections are median in position, usually with only one pit connection, either primary or secondary, between adjacent cells (Figs. 9, 11, 17).

It is difficult to identify the number of chloroplasts per cell. There may be only one variously lobed and dissected chloroplast, or the chloroplasts may be formed through a process of fusion, as has been described for *Drachiella minuta* (J. and G. Feldmann 1950, as *Myriogramme minuta*). In any event, they are convoluted with lobes that extend deep into the interior of the cell (Figs. 14-16). They often appear to be more highly dissected when stained with Aniline blue (Fig. 18) than when stained with hematoxylin.

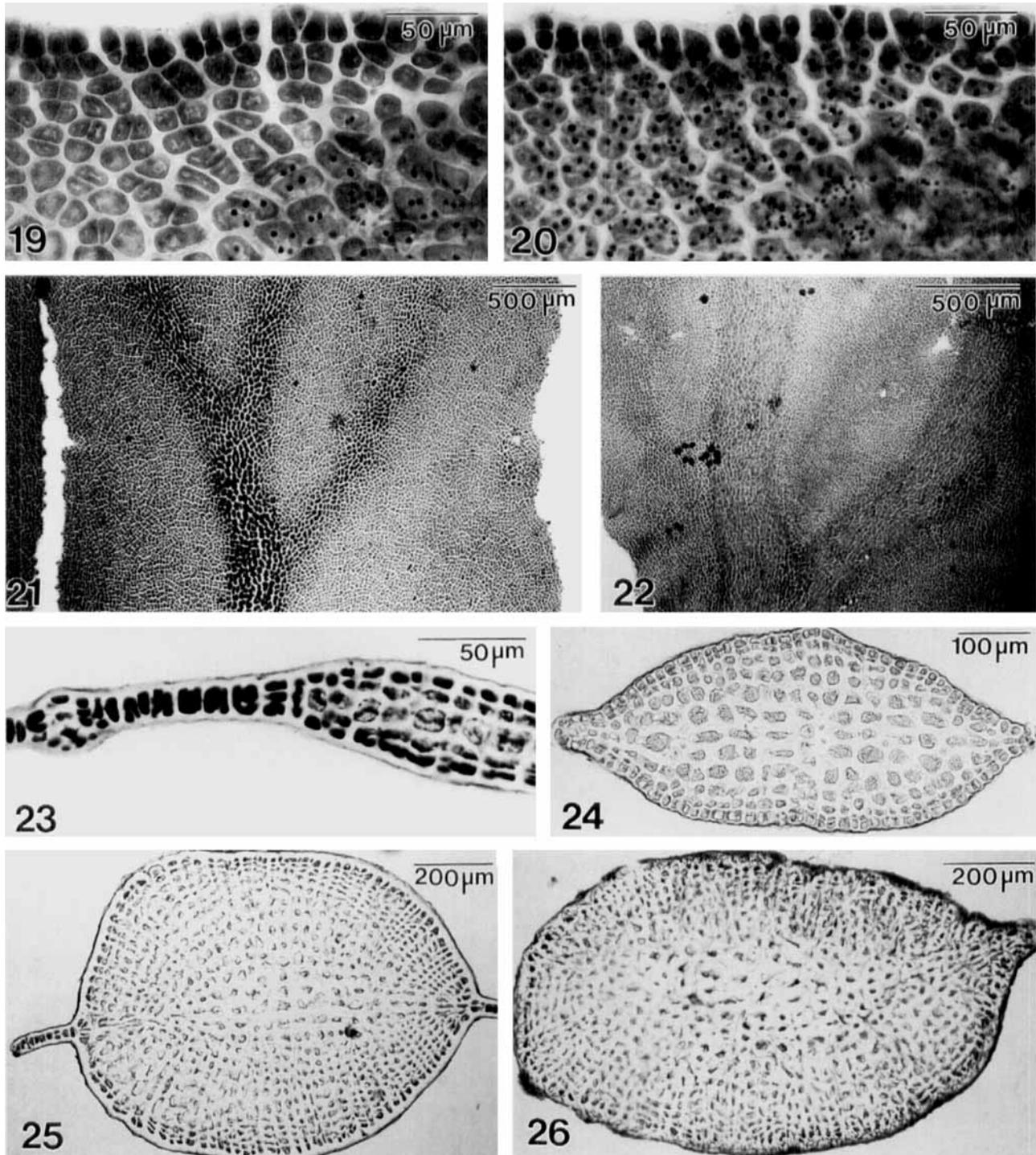
Formation of a midrib or macroscopic nerve begins with periclinal divisions of central cells in the interior of the thallus (Fig. 15). Some of the nuclei migrate toward the thallus surface and come to lie just beneath the chloroplasts. Areas that are becoming tristromatic are readily distinguished in surface



FIGS. 1–8. *Schizoseris condensata*. FIG. 1. Habit of tetrasporangial plant from the drift, Niebla, Chile. FIG. 2. Tip of blade showing acropetal differentiation of nerves and slit formation (arrows). FIG. 3. Bladelet (arrow) proliferating from midrib. FIG. 4. Young proliferation with two apical cells (arrows). FIG. 5. Young bladelet. FIG. 6. Older bladelet with midrib and serrulate margin. FIG. 7. Tip of proliferating bladelet. FIG. 8. Tip of older bladelet. (Figs. 2–8 hematoxylin.)



FIGS. 9–18. *Schizoseris condensata*. FIG. 9. Marginal and intercalary meristems of portion of blade near base of thallus. FIGS. 10, 11. Surface and median optical section of growing margin at tip of blade. FIGS. 12–15. Transverse sections of blades showing distribution of nuclei and chloroplasts: young tip (Fig. 12), older margin (Fig. 13), intercalary portion (Fig. 14), intercalary portion becoming tristromatic (Fig. 15). FIGS. 16, 17. Surface view and median optical section of an internal intercalary meristem. FIG. 18. Chloroplasts in surface view. (Figs. 10–17 hematoxylin, Figs. 9, 18 Aniline blue.)



FIGS. 19–26. *Schizoseris condensata*. FIGS. 19, 20. Surface and median optical section of blade in process of forming a nerve showing distribution of nuclei. FIGS. 21, 22. Young and older midrib and lateral nerves. FIGS. 23–26. Cross-section of developing and mature midribs and nerves. FIG. 23. Three and five-celled stages. FIG. 24. Young midrib showing branched cortical filaments. FIG. 25. Older midrib showing branching of cortical filaments and sharp boundary with monostromatic blade. FIG. 26. Old stipe containing irregularly elongated cells. (Figs. 19, 20 hematoxylin, Figs. 21–26 Aniline blue.)

view with hematoxylin stain, because nuclei that were formerly restricted to the median plane are now seen in the outer periphery of surface cells (cf. Figs. 19 and 20). Polystromatic nerves are indistinct at first (Fig. 2), becoming better defined as they in-

crease in thickness (Figs. 21, 22). The first divisions are largely periclinal with the central cells cutting off cortical initials on either side that divide again (Fig. 23). At about the five-layered stage anticlinal as well as periclinal divisions take place giving rise

to branched cortical files. Divisions are vertical rather than diagonal, such that branches appear slightly offset (Fig. 24). Repeated periclinal divisions along with occasional anticlinal divisions continue increasing the thickness of the rib, and boundaries between the monostromatic blade and polystromatic midrib remain sharp (Fig. 25). Cells become irregularly extended in the oldest midribs and stipes, taking on a rhizoidal appearance (Fig. 26); however, true rhizoids are not formed.

*Male reproduction.* Male plants were not seen in our collections, but they have been described and illustrated by Mendoza (1974). Spermatangia occur on monostromatic and polystromatic portions on both sides of the blade and on leaflets 1–1.5 cm long that proliferate from otherwise denuded midribs. They arise in pairs from parent cells in superficial sori that completely cover a fertile blade.

*Female reproduction.* Procarps are produced randomly among actively dividing cells near the margin at the tips of young blades in roughly equal numbers on either side of the blade. A fertile central cell cuts off pericentral cells on both sides of the thallus; however, only one pericentral cell forms a procarp. One of the nuclei apparently migrates out of the band of nuclei in the median plane of a central cell toward one or the other surface, enlarges, and divides obliquely with the result that one of the daughter nuclei is situated near the surface and the other is seen in the interior of the cell (Fig. 27). The subsequent cell division is also oblique. The resulting pericentral cell is about two-thirds the size of the central cell and is situated on the surface toward one end of it (Fig. 28). The process is repeated, usually involving a different nucleus, and a second pericentral cell is cut off on the opposite side. According to our observations, the procarp is always produced from the first pericentral cell, whereas division of the second pericentral cell yields only vegetative cells. Nuclei that are actively engaged in pericentral cell and procarp formation stain darkly and measure 1.5–2 times larger than vegetative nuclei in the same cell (Figs. 27, 28). They are readily detected under oil immersion by scanning the thallus surface at the level of the chloroplasts, just beneath the outer cell wall.

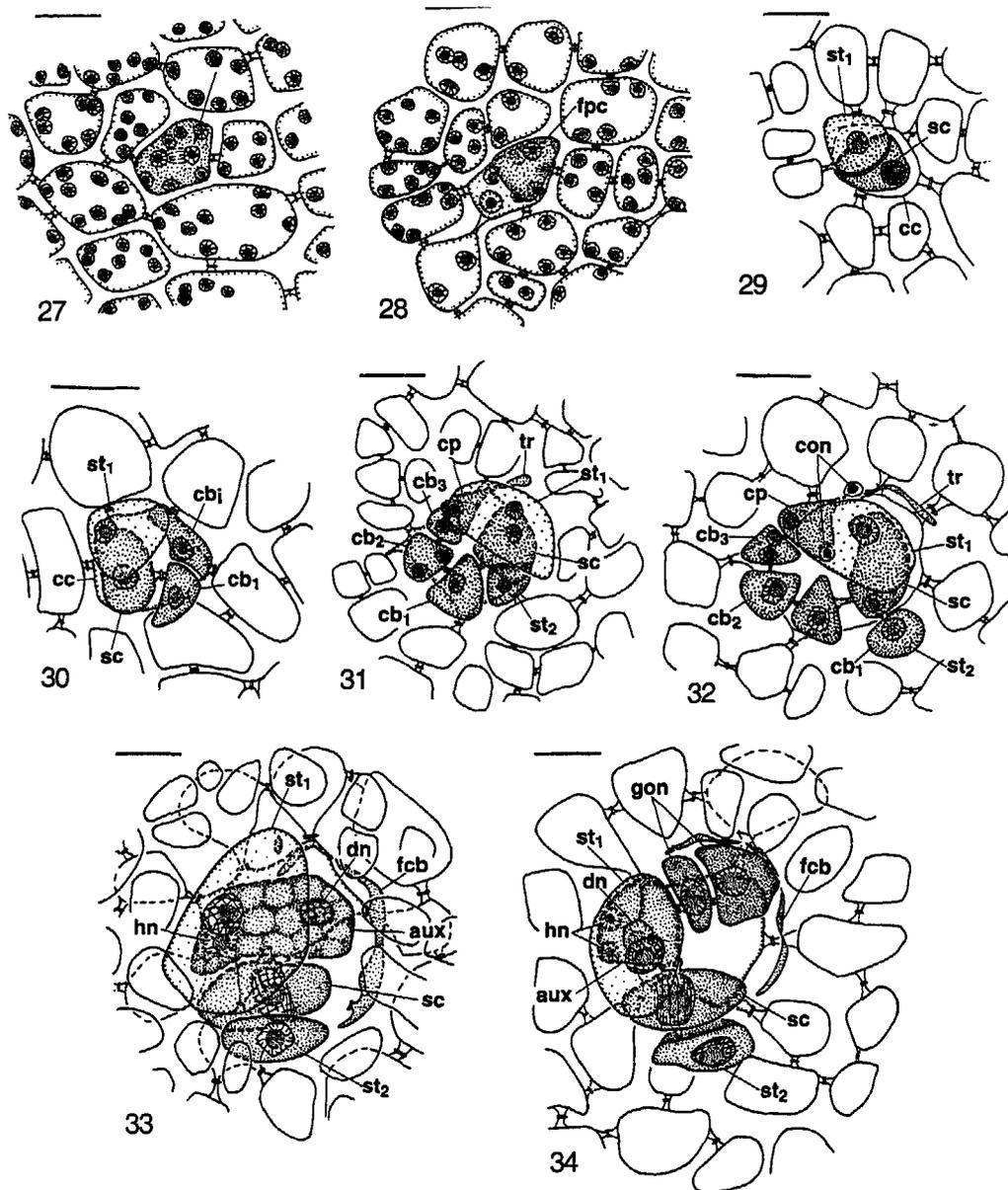
A fertile pericentral cell (= supporting cell) cuts off the first sterile group from its distal end (Fig. 29). The supporting cell next divides laterally by a concavo-convex wall cutting off the carpogonial branch initial, which divides successively twice, first forming a two-celled (Fig. 30) then a three-celled carpogonial branch. At this stage, the supporting cell cuts off a small second sterile group posteriorly by a concavo-convex wall. Finally the third cell of the carpogonial branch divides obliquely cutting off the carpogonium, which is partly covered by the third cell of the carpogonial branch (Fig. 31). The trichogyne elongates beneath the first sterile group and emerges just anterior to it. Orientation of the

procarp is irregular and depends on the orientation of the initial nuclear and cell divisions that give rise to the fertile pericentral cell.

Fertilization was not seen in our material and the earliest postfertilization stages, while present, were not well preserved. Following presumed fertilization the carpogonium divides twice cutting off two minute connecting cells, the first usually distal and the second proximal on the side facing the supporting cell. Each contains a highly condensed nucleus surrounded by a hyaline area and bounding membrane or thin cell wall (Fig. 32). The supporting cell normally divides by a broadly concavo-convex wall cutting off an auxiliary cell terminally that is broader than tall; however, the supporting cell has not divided in the aborted stage shown in Figure 32. The proximal connecting cell fuses with the lateral edge of the auxiliary cell and enlarges upon entry. At this stage, the haploid auxiliary cell nucleus is seen in the lower corner on the side opposite the carpogonial branch (Fig. 33). All four cells of the carpogonial branch fuse after diploidization of the auxiliary cell. The pit connections between them break down, and the nuclei commence to degenerate (Fig. 33). The remnant carpogonial fusion cell takes the form of a thin, barely visible crescent arching around the supporting cell and auxiliary cell until it disappears shortly after gonimoblast initiation (Fig. 34). The two sterile groups normally remain undivided.

The first division of the auxiliary cell is vertical rather than transverse, cutting off a gonimoblast initial on one side (Figs. 34, 36). At the same time, the haploid nucleus divides and one normally sees three nuclei inside the residual auxiliary cell at this stage, one diploid and two haploid nuclei (Figs. 34, 36, 39). The gonimoblast initial divides by concavo-convex septa to produce a curved primary filament directed laterally at right angles to an axis passing through the auxiliary cell, supporting cell and sterile group 2 (Figs. 40, 42). Each segment branches unilaterally toward the convex side (Figs. 42, 43) and upwardly into the cystocarp cavity (Figs. 44, 45). The supporting cell fuses with the remnant of the auxiliary cell (Figs. 40, 42, 43) and with the central cell (Fig. 45), accompanied by the breakdown of primary pit connections. Inner gonimoblast cells fuse progressively with the initial fusion cell at an early stage when the gonimoblasts can still be seen inside a common gelatinous envelope (Fig. 45). Fusions extend laterally incorporating certain of the central cells in the floor of the cystocarp (Figs. 45, 48) and outwardly, incorporating cells of the inner gonimoblast filaments (Figs. 46, 47). Branching continues to be monopodial and unilateral throughout the development of the primary gonimoblasts (Fig. 46) with the formation of a massive highly branched central fusion cell (Fig. 47) bearing carposporangia in terminal branched chains containing a dozen or more carposporangia (Fig. 49).

Sterile group 1 and sterile group 2 remain uni-

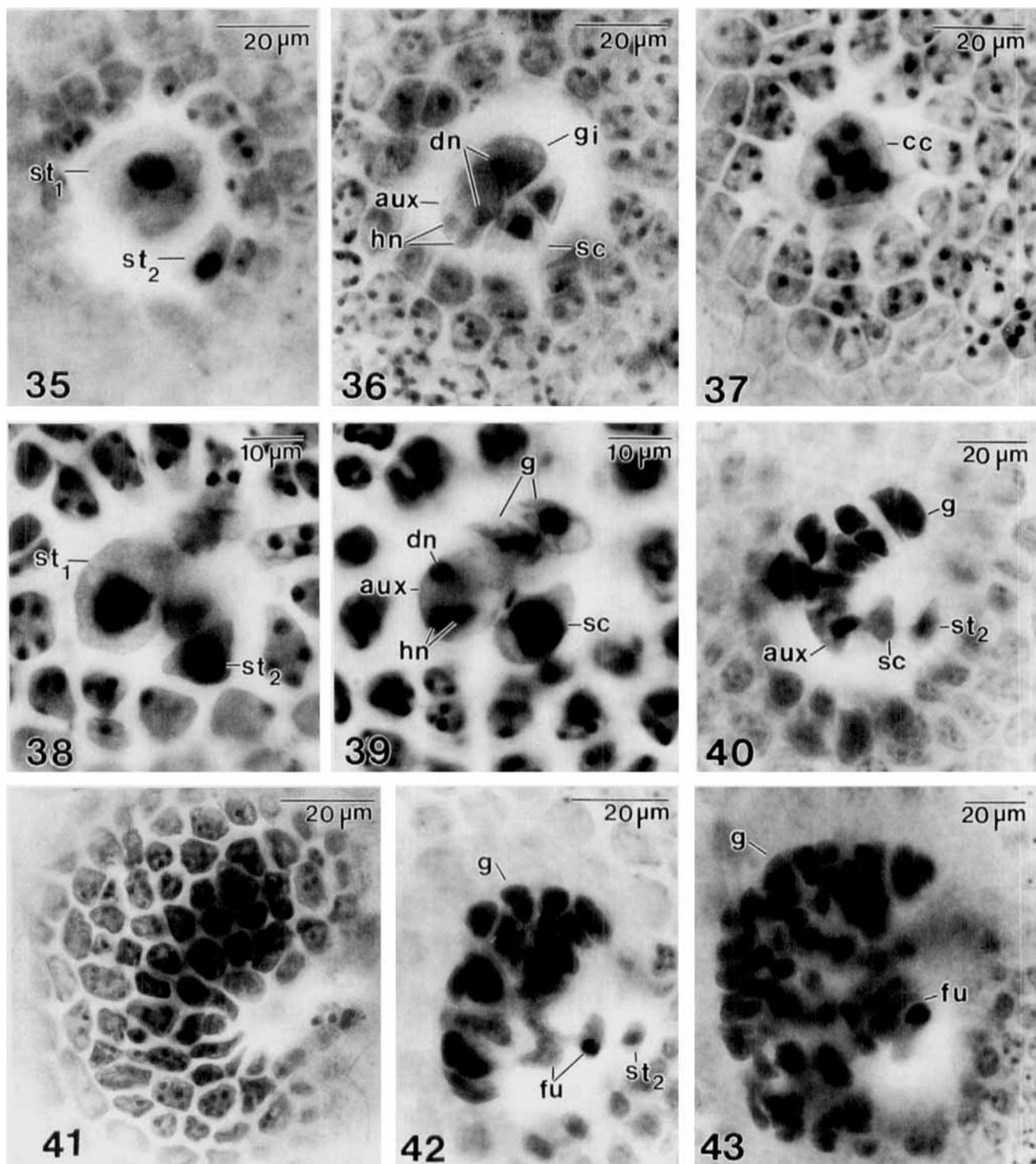


FIGS. 27-34. *Schizoseris condensata*. Scale bars = 10  $\mu$ m. Abbreviations: aux = auxiliary cell, cc = central cell, con = connecting cell, cb<sub>1</sub>, cb<sub>2</sub>, cb<sub>3</sub> = cells of the carpogonial branch, cb<sub>i</sub> = carpogonial branch initial, cp = carpogonium, dn = diploid nucleus, fcb = fused carpogonial branch, fpc = fertile pericentral cell, gon = gonimoblast, hn = haploid nucleus, sc = supporting cell, st<sub>1</sub> = sterile group 1, st<sub>2</sub> = sterile group 2, tr = trichogyne. FIG. 27. Stage in nuclear division in a central cell (arrow) leading to formation of a fertile pericentral cell. FIG. 28. Uninucleate fertile pericentral cell. FIG. 29. Supporting cell bearing sterile group 1. FIG. 30. Developing procarp showing supporting cell bearing sterile group 1 and a two-celled carpogonial branch. FIG. 31. Mature procarp showing a supporting cell bearing two sterile groups and a four celled carpogonial branch. FIG. 32. Postfertilization stage showing carpogonium with two connecting cells. The supporting cell has not divided. FIG. 33. Fused carpogonial branch and auxiliary cell containing a haploid and a diploid nucleus. FIG. 34. Two-celled gonimoblast and remnant auxiliary cell containing one diploid and two haploid nuclei. (Figs. 27-34 hematoxylin.)

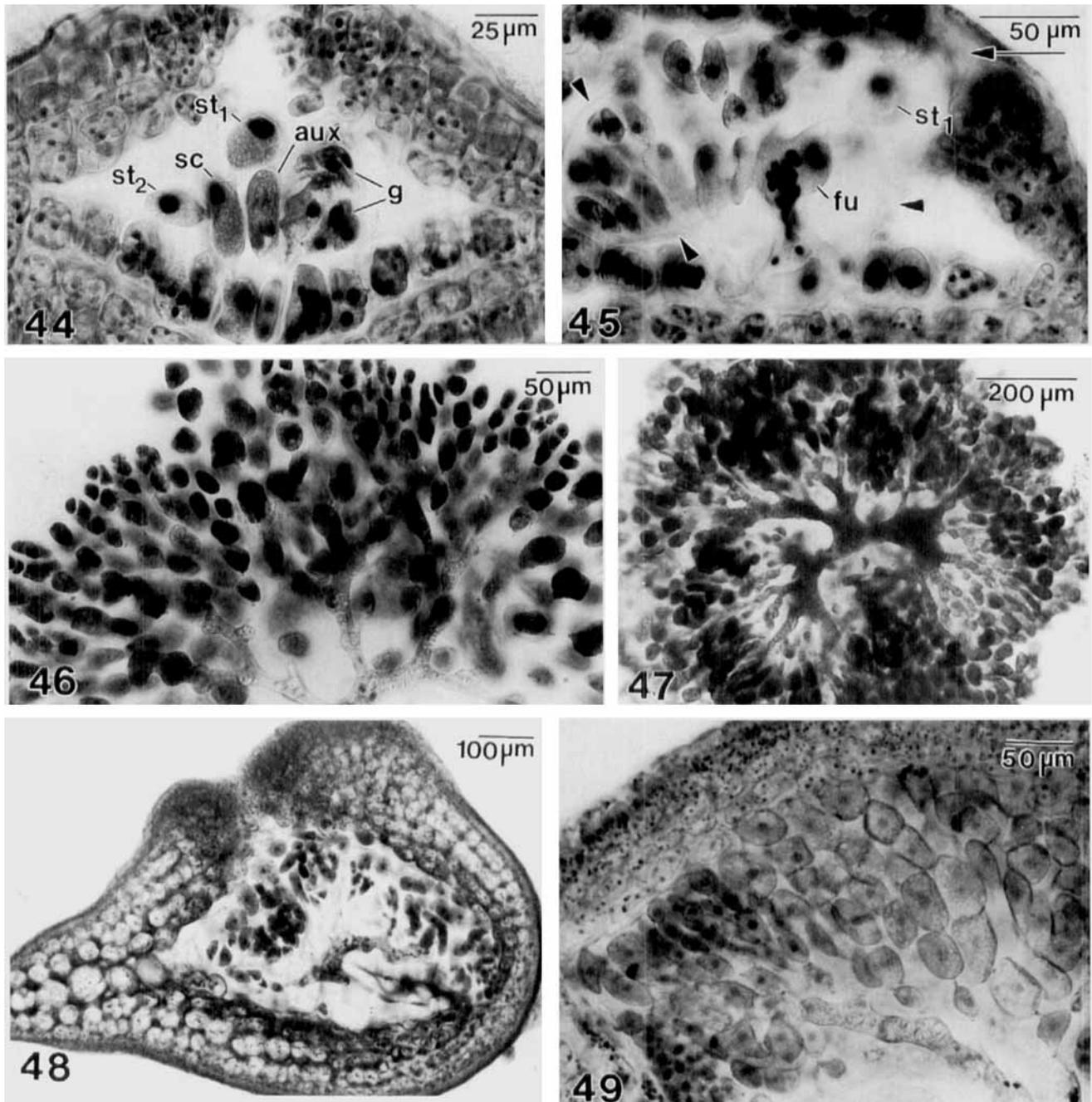
cellular, each containing a single greatly enlarged nucleus (Figs. 35, 38, 44). Pit connections between the supporting cell and the sterile groups break down; however, each retains its autonomy and shape (Figs. 44, 45). Sterile group 1 often detaches before finally degenerating (Fig. 45). An ostiole forms directly above the first sterile group, which is often positioned off center in relation to the developing gonimoblasts (Figs. 41, 45, 48).

Vegetative cells surrounding the young gonimo-

blasts first divide periclinally coupled with occasional anticlinal divisions to produce a pericarp four to six cell layers in thickness. Nuclear divisions are oriented perpendicular to the plane of the blade and nuclei that earlier were restricted to the median plane appear at the level of the chloroplasts beneath the outer cell wall (Figs. 35, 38). The cystocarp cavity forms by separation of the pericarp filaments from the bearing central cells in the floor of the cystocarp. The mucilaginous material appears to come



FIGS. 35–43. *Schizoseris condensata*. FIGS. 35–37. Three optical sections of stage with gonimoblast initial. FIG. 35. Surface view showing sterile group 1 (*st*<sub>1</sub>) and sterile group 2 (*st*<sub>2</sub>). FIG. 36. Intermediate level showing supporting cell (*sc*), remnant auxiliary cell (*aux*) with one diploid (*dn*) and two haploid (*hn*) nuclei and the gonimoblast initial (*gi*) with a nucleus in metaphase. FIG. 37. Median optical section showing the multinucleate central cell that bears the procarp. FIGS. 38, 39. Two optical sections of stage with two gonimoblast cells. FIG. 38. Surface view showing sterile group 1 (*st*<sub>1</sub>) and sterile group 2 (*st*<sub>2</sub>). FIG. 39. Supporting cell (*sc*), residual auxiliary cell (*aux*) containing one diploid (*dn*) and two haploid (*hn*) nuclei and a two-celled gonimoblast (*g*). FIG. 40. Unilateral development of gonimoblasts (*g*), and partly fused residual auxiliary cell (*aux*), supporting cell (*sc*), and sterile group 2 (*st*<sub>2</sub>). FIGS. 41, 42. Two optical sections of a developing cystocarp. FIG. 41. Pericarp with ostiole off center. FIG. 42. Gonimoblasts (*g*), fusion cell (*fu*), and remnant sterile group 2 (*st*<sub>2</sub>). FIG. 43. Optical section of gonimoblasts (*g*) and early fusion cell (*fu*). (Figs. 35–43 hematoxylin.)

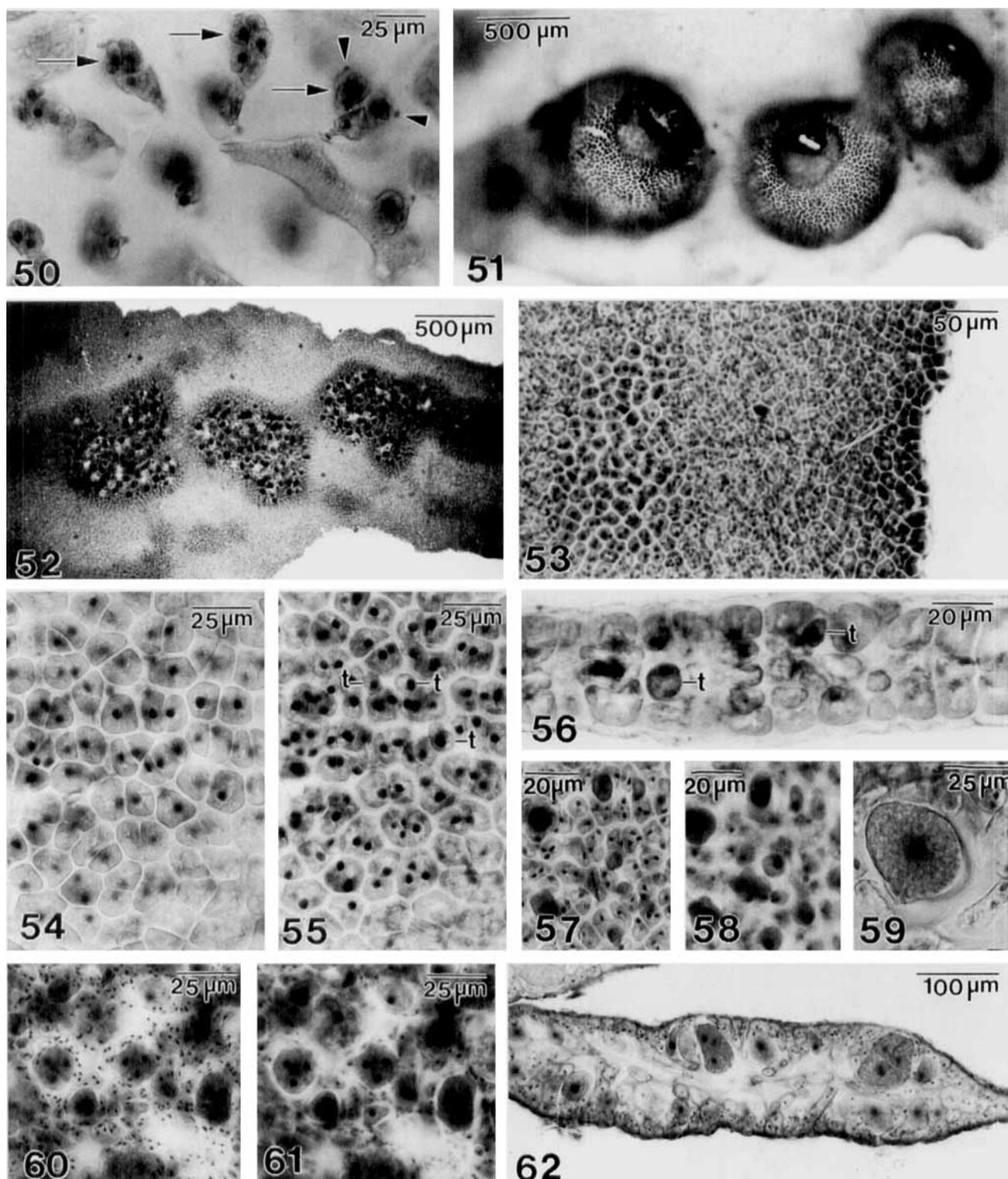


FIGS. 44–49. *Schizoseris condensata*. FIG. 44. Early postfertilization stage seen in cross-section showing supporting cell (sc), sterile group 1 ( $st_1$ ) and sterile group 2 ( $st_2$ ), the residual auxiliary cell (aux), and young gonimoblasts (g) in relation to the pericarp and ostiole and cells with enlarged nuclei in floor of cystocarp. FIG. 45. Young gonimoblasts developing unilaterally inside a common gelatinous envelope (arrowheads) showing early fusion cell (fu), remnant sterile group 1 ( $st_1$ ), and ostiole (arrow on right). FIG. 46. Immature, unilaterally branched carposporangial chains borne on fused gonimblast filaments. FIG. 47. A young cystocarp as seen from above after excision of pericarp showing fusion cell and carposporangial chains. FIG. 48. Cross-section of young cystocarp showing fusion cell, carposporangial chains and ostiole off center. FIG. 49. Cross-section showing unilaterally branched chains of mature carposporangia borne on fused gonimblast filaments. (Figs. 44–49 hematoxylin.)

from the sterile groups and cells in the floor of the cystocarp outside the gonimblast envelope (Fig. 45).

Some older cystocarps were observed to produce secondary gonimoblasts. These arise through division of unfused basal gonimblast cells that remain

attached to the gonimblast fusion cell after carposporangia mature and are released (Fig. 50). The nature of these cells is evident because each contains one or two distal septal plugs, which are the remnants of pit connections that formerly linked them to the carposporangial chains. Our material



FIGS. 50–62. *Schizoseris condensata*. FIG. 50. Clusters of secondary carposporangia (arrows) developing from sterile cells at base of released carposporangial chains. (The positions of remnant pit connections are indicated by arrowheads.) FIG. 51. Cystocarps with slitlike ostioles in surface view. FIGS. 52–62. Tetrasporangial development. FIG. 52. Tetrasporangial sori. FIG. 53. Young sorus developing inside thallus margin. FIGS. 54, 55. Surface view and optical section of a developing sorus showing the origin of the tetrasporangia (t) from inner cortical cells. FIG. 56. Cross-section of young tetrasporangial sorus showing position of tetrasporangia in relation to inner cortical and surface cells. FIGS. 57, 58. Surface view and optical section of young tetrasporangial sorus after the cortical cells have divided anticleinally. FIG. 59. Cross-section showing young tetrasporangium attached to inner cortical cell. FIGS. 60, 61. Surface view and optical section of sorus containing tetrahedrally divided tetrasporangia and much divided surface cortical cells. FIG. 62. Transverse section of sorus containing young and mature tetrasporangia on both sides of central cells. (Figs. 50–62 hematoxylin.)

did not contain mature secondary carposporangia, and the fate of the secondary gonimoblasts is unknown.

A mature cystocarp measures nearly a millimeter in diameter at its base, is strongly emergent and bulbous with a prominent collar and slitlike ostiole (Fig. 51). Nerves differentiate toward young developing cystocarps and cystocarps are commonly seen distributed alongside or at the ends of nerves, as illustrated by Ricker (1987: fig. 119d).

*Tetrasporangial development.* Tetrasporangia develop in sori on both sides of blades, primarily from monostromatic regions within the margins (Figs. 52, 53) alongside the midribs and nerves (Ricker 1987: fig. 119e), or they may spread across their outer surfaces. Initiation of a tetrasporangial sorus begins with reorientation of nuclear divisions such that dividing nuclei lie in the outer surface of a cell just beneath the chloroplasts (Figs. 54, 55). Periclinal cell divisions similar to those that give rise to young nerves initially produce soral areas five layers thick (Fig. 56). The tetrasporangia are cut off laterally from cells of the inner cortical layer on either side of the central layer, which remains sterile (Fig. 56). Young tetrasporangia are completely covered by cortical cells at the time of their initiation (Figs. 54, 55). The surface cells divide anticlinally maintaining a continuous cover of progressively smaller cells as the tetrasporangia enlarge and divide (Figs. 57, 58, 60, 61). Primary tetrasporangia arise from the innermost cortical cells (Fig. 59), whereas secondary tetrasporangia are cut off progressively from cells closer to the thallus surface (Fig. 62). Tetrasporangial sori that overlie a vein normally develop on only one side. A tetrasporangium divides simultaneously into four tetrahedrally-shaped tetraspores (Figs. 60–62).

#### DISCUSSION

Hommersand and Fredericq (1997) determined that, whereas Kylin (1924) had established *Myriogramme* upon *M. livida* (J. D. Hooker et Harvey) Kylin, he based his characterization of *Myriogramme* and the Myriogramme group primarily on his observations of *M. minuta* Kylin, a newly described species from Naples, Italy. This species has since been transferred to *Drachiella* as *D. minuta* (Kylin) Maggs et Hommersand. *Drachiella minuta* possesses a suite of characters that distinguishes it unambiguously from *Myriogramme* and allies it instead with *Schizoseris*. Thus, important characters listed by Kylin in his description of the Myriogramme group apply to the Schizoserideae as proposed here, not to the Myriogrammeae of Hommersand and Fredericq (1997). All of the taxa listed under "Specimens of Other Taxa Examined" possess characters that are diagnostic for the Schizoserideae.

Kylin (1924:102–105) identified three groups in the Nitophylloideae in which growth at the thallus apex does not involve a transversely dividing apical cell: the Myriogramme group, the Nitophyllum

group, and the Cryptopleura group. With the establishment of the tribes Myriogrammeae and Schizoserideae, four assemblages are recognized that lack transversely dividing apical cells. Table 1 summarizes the distinguishing features that characterize each of the four assemblages based on a survey of the literature and our own observations.

Advanced members of the Delesseriaceae, including all Nitophylloideae, possess intercalary meristems in addition to a transversely dividing apical cell or a row of marginal meristematic cells. Regions of cell division are succeeded by areas of cell maturation in most, and the greater part of the thallus is composed of mature tissues. In contrast, *Schizoseris condensata* is representative of an extreme behavior in which monostromatic portions of the thallus are composed almost entirely of actively dividing meristematic cells. The only cells that expand and cease divisions are those found at the base or in the central areas of midribs and nerves. Under conditions of extreme abrasion, these may be the only parts that persist, with regeneration occurring through the proliferation of secondary bladelets. Male plants of *Schizoseris condensata* described by Mendoza (1974), for example, consist largely of primary ribs and nerves covered by fertile proliferations.

Thallus shape is due primarily to a rapid rate of intercalary growth, combined with progressive acropetal differentiation of midribs and nerves and regular formation of slits parallel to the lateral margins that result in laciniae and the sloughing off of portions of the blades. The marginal meristem functions primarily to maintain and repair the thallus border in the face of rampant growth and laciniae formation, hence its irregularly serrulate appearance.

Species and genera related to *Schizoseris condensata* have similarly irregular margins and small-celled intercalary meristems and tissues. Larger, coarser varieties of *Schizoseris* from the southern hemisphere that range in habit from broadly membranous types with fine nerves, deeply dissected forms with coarse nerves to variously lacinate forms with coarse midribs and lateral nerves, and proliferous forms were combined under a single species, *Schizoseris dichotoma* (J. D. Hooker et Harvey) Kylin by Ricker (1987). Our studies have not added any new information relevant to the solution of this problem.

*Neuroglossum binderianum* Kützing from South Africa (Wagner 1954), a large, subdichotomously branched species with a prominent midrib and abundant proliferations, is very similar to *Schizoseris* in the behavior of its meristem and manner of vegetative growth. At the other extreme, *Abroteia orbicularis* from New Zealand (Wagner 1954) is a diminutive epiphyte on *Carpophyllum maschalocarpum*, a brown alga of exposed habitats. The stipe is brief, and midribs and nerves are absent; however, the entire blade is actively meristematic composed of small cells bordered by an irregular, serrulate margin.

TABLE 1. Characters of four groups of the Delesseriaceae/Nitophylloideae that lack a transversely dividing apical cell.

	Myriogrammeae	Schizoserideae	Cryptopleura group	Nitophyllum group
1. Meristems	Marginal and intercalary	Mostly intercalary	Marginal and intercalary	Marginal and intercalary
2. Nuclear distribution in meristematic cells	Medial	Medial	Medial	Parietal
3. Nuclear distribution in mature cells	Alongside lateral walls	Initially medial, later parietal	Parietal, mostly beneath chloroplasts	Parietal, randomly distributed
4. Secondary pit connections	Few, largely medial	Few, medial, later some superficial	Few, largely medial	Numerous, medial and superficial
5. Chloroplasts	Numerous, platelet- to sausage-shaped	Few, lobed, dissected, separate or fused	Numerous, mostly small platelets	Abundant, small platelets or bead-like
6. Microscopic veins	Absent	Absent	Usually present	Present in some
7. Macroscopic nerves, tri- to polystromatic	Present, extensive to basal only	Present, extensive to basal only	Present, extensive to basal only	Basal only, or absent
8. Anatomy of macroscopic nerves	Cortical files unbranched, in horizontal tiers and vertical rows	Cortical files branched, the cells progressively smaller toward surface	Cortical files branched or unbranched, in tiers and rows	Cortical files little branched, mostly in tiers and rows
9. Spermatangial sori	Produced in monostromatic areas	Produced in mono- and polystromatic areas	Produced in mono- and polystromatic areas	Produced in monostromatic areas
10. Procarp cover cells	Present, distal	Absent	Absent	Present, lateral
11. Sterile groups	2, 1-celled	2, 1-celled	2, 1-2-celled	1, 1-3-celled, lateral
12. Carpogonial branch	Curved, trichogyne emerging proximal to cover cells	Curved, trichogyne emerging from beneath sterile group 1	Curved, trichogyne emerging lateral to sterile group 1	Slightly curved, flanked by cover cells and sterile group
13. Orientation of gonimoblast initial	Distal with transverse and lateral divisions	Lateral, branching initially unilateral	Distal, with several transverse divisions	Distal, young gonimoblast globular
14. Arrangement of carposporangia	In branched chains, or terminal and either successional or solitary	In branched chains or clusters	Mostly terminal and maturing in basipetal succession	Sequential and either terminal or in short branched chains
15. Fusion cell	Large, highly branched	Large, highly branched	Moderate size, compact	Small and basal
16. Origin of first tetrasporangia	From central cells	From cortical cells	From cortical or central cells	From cortical or central cells

The thallus margin is relatively persistent in *Drachiella minuta*; however, this species also possesses the *Schizoseris* type of marginal and intercalary meristems (Maggs and Hommersand 1993).

The *Schizoseris* assemblage is characterized by a combination of unique cytological characters. Most prominent is the presence of one to few dissected chloroplasts with lobes that extend deep into the cell interior. This character was first seen in *Drachiella minuta*, where it has been described in detail by J. and G. Feldmann (1950, 1975) and Magne (1957) (as *Myriogramme minuta*). J. and G. Feldmann (1950) observed that a single chloroplast forms in germlings through fusion of many separate chloroplasts, and Magne (1957) demonstrated that cells isolated from the middle layer of tristromatic portions of the thallus contained numerous plastids. When cells from this layer were isolated manually and maintained for a while in running seawater, the plastids multiplied and fused into a single, continuous, ribbon-shaped plastid. Finally, J. and G. Feldmann (1975) showed with electron microscopy that the lobed plastid of *Drachiella minuta* (as *Myriogramme minuta*) encases a mass of minute vacuoles and that

internal cells possess several plastids surrounded by distinctive elongate amyloid bodies. Formalin-preserved material of *Schizoseris condensata* and other species investigated also contained unusual cell inclusions that resembled those seen in *Drachiella minuta*. These features need to be characterized.

The nuclei in meristematic cells of *Schizoseris condensata* amass, sometimes in large numbers, in the median plane of the cell, and are redistributed toward cell surfaces only when a region becomes polystromatic. The nuclei have the same distribution and appearance in the other genera and species listed under "Specimens of Other Taxa Examined." Likewise, there is usually just one primary or secondary pit connection between adjacent cells in meristematic tissues. Mature, fully differentiated cells have their nuclei redistributed more or less randomly around the periphery of the cell next to the chloroplast. In *S. condensata*, this occurs only in midribs and nerves in vegetative blades, whereas in *Drachiella* redistributed nuclei are encountered in mature monostromatic, tristromatic and polystromatic regions (pers. observ.). Additional secondary

pit connections may form at this time, often becoming numerous.

Taken together, the cytological characters and patterns of vegetative growth that characterize the Schizoserideae are distinct, and serve to separate this group from all other Delesseriaceae that lack transversely dividing apical cells. Members of the Cryptopleura group, the Nitophyllum group, and the tribe Myriogrammeae all possess windowlike cells that are highly vacuolate when mature (Maggs and Hommersand 1993, Hommersand and Fredericq 1997). The chloroplasts become dissected forming platelets or discs, the nuclei and secondary pit connections are arranged in different patterns, and vegetative growth takes the form of a continuous progression from meristematic to mature tissues (Table 1).

**Reproductive development.** Spermatangial and tetrasporangial sori are produced primarily in undifferentiated meristematic areas in *Schizoseris condensata* and other members of the Schizoserideae. This behavior stands in contrast to that found in the Myriogrammeae, the Nitophyllum group, and typical members of the Cryptopleura group in which spermatangial and tetrasporangial sori are formed primarily through the resumption of meristematic activity in otherwise mature tissues (Table 1, Maggs and Hommersand 1993, Hommersand and Fredericq 1997). Tetrasporangia are cut off laterally from inner cortical cells and less frequently from primary, central cells and are arranged in two layers or irregularly dispersed and covered by an outer cortical layer.

It is, however, in the development of the procarp before and after fertilization that the most dramatic differences are encountered that set the Schizoserideae apart from other assemblages in the Delesseriaceae. Procarps are exceedingly compact in *Schizoseris condensata*, as they are in *Drachiella minuta* (Kylin 1924, as *Myriogramme minuta*), *Neuroglossum binderianum* (Wagner 1954), and *Abroteia orbicularis* (Wagner 1954). This is because the fertile central cells have recently divided and are quite small at the time of procarp initiation. Procarps initiated by a central cell differentiate on only one side of the thallus and a procarp is normally absent on the opposite side. Where the procarps are formed randomly on either side of the thallus, as in *Schizoseris*, *Neuroglossum* and *Abroteia*, cystocarps are seen on both sides of the thallus. In *Drachiella minuta*, however, procarps and cystocarps are formed only on the upper side of the blade (Magne 1957, as *Myriogramme minuta*) and thalli are dorsiventral with respect to this character. The carpogonial branch is strongly curved with the trichogyne extending beneath sterile group 1 and emerging distally to it. Kylin (1924) who discovered this feature in *Drachiella minuta* (as *Myriogramme minuta*) especially stressed its diagnostic importance. The procarp in members of the Cryptopleura group (Kylin 1924, Papenfuss 1939, Wagner 1954) is simi-

lar in size and shape to that seen in the Schizoserideae; however, the carpogonial branch and trichogyne emerge alongside sterile group 1 instead of passing beneath it (Table 1).

Diploidization of the auxiliary cell involves the union of the auxiliary cell with one of two connecting cells in *Schizoseris condensata*, as in all other Delesseriaceae we have examined. The first division of the auxiliary cell is vertical rather than transverse and the initial branching is lateral to one side. Growth of the gonimoblasts is monopodial with the subsequent branching primarily unilateral. Unilateral branching is commonplace in the Delesseriaceae but does not extend to include the first division of the auxiliary cell in any other group that we are aware of. The orientation of the first division and early development of the gonimoblasts is identical in the species of *Schizoseris*, *Neuroglossum*, and *Abroteia* that we have investigated and by extrapolation appear to be the same in *Drachiella minuta*, as illustrated by Magne (1957, as *Myriogramme minuta*). The sterile groups remain undivided after fertilization in most instances and divide only once in *Drachiella minuta* (Magne 1957, as *Myriogramme minuta*). Pericarps are raised with a prominent collar and a single ostiole that is often situated off center, as in *Schizoseris condensata*.

The massive fusion cell with its bulbous central base, radiating fusion processes incorporating central cells across the floor of the cystocarp, and candelabra-like fused gonimoblasts bearing carposporangia in branched chains is one of the more striking features of the Schizoserideae. This distinguishing character has been described or illustrated previously for *Schizoseris* (Kylin 1924, Ricker 1987), *Neuroglossum* (Wagner 1954) and *Drachiella minuta* (Magne 1957, as *Myriogramme minuta*), and is seen as well in *Abroteia orbicularis* (pers. observ.).

#### TAXONOMIC CONCLUSIONS

All of the genera and species treated here as relatives of *Schizoseris condensata* were previously placed in the Myriogramme group by Kylin (1924, 1956). We propose a new tribe, the Schizoserideae, to contain *Schizoseris* Kylin 1924, *Neuroglossum* Kützing 1843, *Abroteia* J. Agardh 1876, and provisionally *Polycoryne* Skottsberg in Kylin and Skottsberg 1919. The taxonomic position of *Platyclinia* J. Agardh 1898 is left unresolved. The diagnosis given below is based on a study of the genotype and on species listed in this paper under "Specimens of Other Taxa Examined."

#### **Schizoserideae** Hommersand et Fredericq trib. nov.

*Thallus foliosus, praecipue monostromaticus polystromaticis basibus, stipitibus, nervibus macroscopicis aut venibus grossis, aut tristromaticis ad polystromaticas praeter marginem, tum plerumque sine nervibus conspicuis. Veni microscopici absentes. Incrementum diffuse meristematis*

*marginalibus intercalaribusque. Spissationes nervorum et stipitis formantes combinatione divisionum periclinarum anticlinarumque. Cellulae continentem simplicem chloroplastum parietalem varie lobatum, convolutum, aut dissectum in taenias, aut continentem plures chloroplastos probabiliter metastabiles, frangentes et coalescentes causas variantes. Nuclei 1-numerosi, dispositi in lamella per transverse medianum cellulae in cellulas juvenes, dispersi varie in cellulas maturas in telas veteres. Synapsis primae et secundae prominentes, medianae, usually 1 inter contiguas cellulas; synapsibus formatis postea secundis tenuibus formatis ad superficiem laminae in partes veteres thalli. Spermatangia in soros separatos aut aggregatos in partes monostromaticas aut polystromaticas thalli. Procarpia genita singularia in alteruterum latus thalli, aut solum in superficiem supernam in aliquot, circumferentia circulari constantia ex cellula sustinente praebenti amplam lateralem turmam sterilem 1- (2)-cellularem, filum carpogoniale quadricellulare trichogyna peragrata subter turmam sterilem lateralem emergenti positione antica, et turma basali sterili. Cellula auxiliaris latior quam alta, diploidatur cellula conjunctiva dividens verticaliter in initium gonimoblasti laterale et residualem cellulam auxiliarem; filamenta gonimoblasti initio genita unilateralia in arcu, postea radiata in directiones omnino et praebentia carposporangia in simplices aut catenatas ramosas; cellula fusionalis extensiva, similis candelabrae, incorporans turmas steriles, cellulas in pavimento cystocarpium, plerumque cellulas steriles gonimoblasti; pericarpium 4-6-stromaticum ostiolo excentrali, tegenti sterilem turmam-1. Tetrasporangia in soros parvos circulares, aut sori aggregati, tetrasporangia primaria genita e cellulis corticalibus, plerumque disposita in strata duo circumcincta per cellulas corticales; cellulae secundae genitae e cellulis corticalibus interdumque cellulis centralibus. Tetrasporangia tetraedrica divisa.*

Genus typicum: *Schizoseris* Kylin 1924.

Plant body foliose, primarily monostromatic with polystromatic bases, stipes and macroscopic nerves, or tristromatic to polystromatic except at or near the margin, and then usually lacking conspicuous nerves. Microscopic veins absent. Growth diffuse, by marginal and intercalary meristems. Nerve and stipe thickenings typically formed by a combination of periclinal and anticlinal divisions. Cells containing a single parietal chloroplast that is variously lobed, convoluted or ribbonlike, or several chloroplasts present, probably metastable, breaking up and fusing under different conditions. Nuclei 1-many, arranged in a plate across the middle of the cell in young cells, variously dispersed in mature cells in older tissues. Primary and secondary pit connections conspicuous, median, usually one between each adjacent cell; later-formed secondary pit connections minute, infrequent to abundant at cell surfaces in older parts of blade. Spermatangial sori separate or aggregated on monostromatic or polystromatic portions of blade. Procarps formed singly near margins on either side of thallus, or only on upper surface in some, circular in outline consisting of a supporting cell bearing a large 1- (2)-celled lateral sterile

group, a strongly curved 4-celled carpogonial branch in which the trichogyne traverses beneath the lateral sterile group emerging anterior to it, and a small, 1- (2)-celled basal sterile group. Auxiliary cell broader than tall, diploidized by a connecting cell and dividing vertically into a lateral gonimoblast initial and residual auxiliary cell; gonimoblast filaments at first developing unilaterally in an arc to one side, later radiating in all directions and bearing carposporangia in simple or branched chains; fusion cell extensive, candelabra-like, incorporating sterile groups, cells in floor of cystocarp, and most sterile gonimoblast cells; pericarp 4-6 cell layers thick with the ostiole typically off center, overlying the first sterile group. Tetrasporangia in small circular sori, or the sori confluent; primary tetrasporangia arising from inner cortical cells, usually disposed in two layers surrounded by cortical filaments; secondary tetrasporangia arising from cortical cells and sometimes from central cells. Division of tetrasporangia tetrahedral.

Type genus: *Schizoseris* Kylin 1924.

It should be noted that J. Agardh (1898:99) had previously established the Neuroglosseae at what would now be recognized as the tribal level; however, J. Agardh's Neuroglosseae is invalid in accordance with Article 33.5 of the International Code of Botanical Nomenclature (Greuther 1994) because he designated the rank as section, which is an infrageneric rather than an infrafamilial category.

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